

Aspects of the breeding biology, migratory
movements, winter survival, and population
fluctuations in the Great Tit *Parus major*
and the Blue Tit *P. caeruleus*

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Abstract. Various aspects of the ecology of the Great and the Blue Tit, especially those relating to breeding biology and population fluctuations, were studied in a population breeding in nestboxes near Lund, southernmost Sweden. One major problem in these and other species of birds concerns the timing of egg laying; the tits responded to food supplementation by laying earlier, as predicted from one of the main hypotheses. Yet, no selective advantage of early breeding was identified. Clutch size remained fairly constant over the period when first clutches were produced, with some tendency towards fewer eggs in the very earliest clutches, while second clutches decreased strongly in size with the progress of the season. Losses were small in first, but large in second clutches. Both female and nestling weights were only weakly influenced, and female survival independent of brood size, indicating a high degree of individual adjustment of clutch size. Juvenile disappearance rate seemed to be highest during the first period after nest-leaving and remained high until winter. The numbers of Great and Blue Tits recorded on autumn migration were an increasing function of population density, as measured in the preceding breeding season. Migratory movements in these species are unlikely to be governed by the availability of beech mast, as previously suggested, because the relation to density was apparent also outside the distribution range of the beech. Breeding populations of tits, and some other passerines, were positively correlated with temperature in the preceding winter, temperature, or some factor associated with it, probably acting via food; winter feeding increased the Great Tit population in one year compared to controls, but not in another with beech mast.

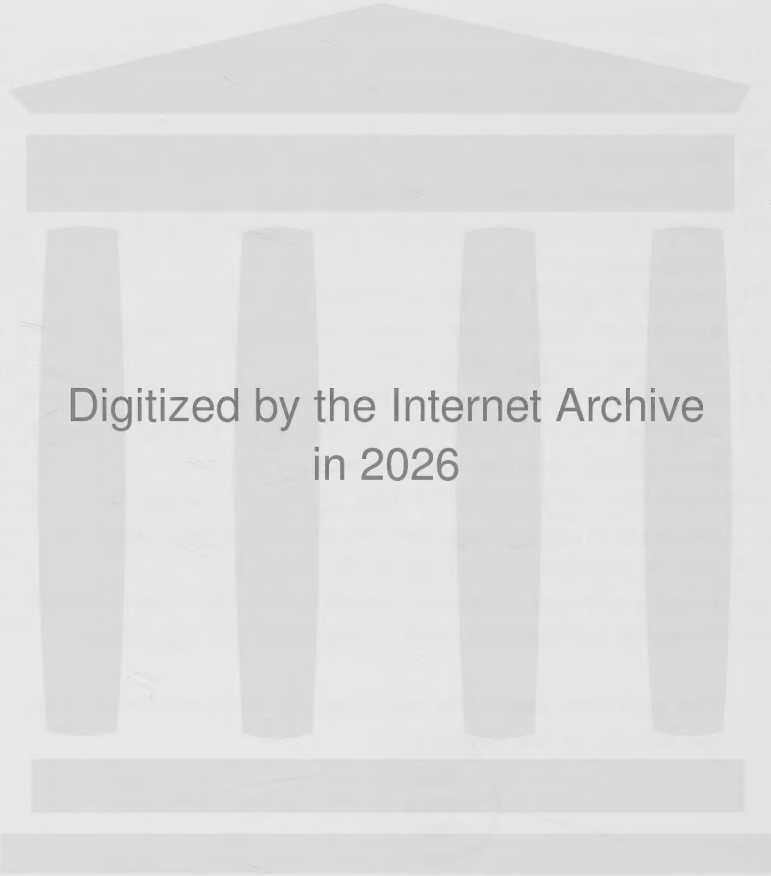


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Förord

Det fältarbete, varpå denna avhandling huvudsakligen bygger, påbörjades våren 1969, och de allra sista fältdata insamlades våren 1978. Dräktighetstiden har således varit lång. När nu barnet äntligen har krystats fram, tvingas jag detta till trots konstatera, att det bär tydliga spår av prematur födsel. Den främsta anledningen till att så lång tid förflutit mellan fältarbetets avslutande och avhandlingens färdigställande är, att jag som redaktör för Vår Fågelvärld under flera år i första hand sysselsatt mig med andras manus. Under samma tidsperiod har jag också höjt min egen genetiska fitness, vilket också satt sina spår i (det uteblivna) avhandlingsarbetet. Det finns också en tredje anledning till det långsamma framåtskridandet, nämligen att mitt intresse för beteendeeekologiska frågor egentligen varit större än mitt intresse för de renodlat populationsdynamiska.

Av den just nämnda anledningen har jag speciellt uppskattat de regelbundna diskussionsträffar, som under de senaste terminerna hållits inom den beteendeeekologiska gruppen vid avdelningen. Något jag mycket saknade under de år jag på grund av redaktörssysslan endast sporadiskt besökte avdelningen, var den gemytliga stämning, ofta karakteriserad av stimulerande och stundom minst sagt engagerade diskussioner, som rått i de olika lunch- och kaffegrupper jag frekventerat under årens lopp. Trots att jag inte är någon inbiten kaffeälskare, tvingas jag konstatera att de väsentligaste forskningsresultaten och forskningsidéerna utformas på kafferummen - under det senaste halvåret har jag också tagit fasta på detta, vilket säkert en del av mina kolleger konstaterat med förfäran när de hört talas om tidsplanen för denna avhandling.

Självfallet står jag i tacksamhetsskuld till en hel rad personer, såväl inom som utanför avdelningen, därför att de på olika sätt bidragit med hjälp eller stimulans. De är dock alltför många för att alla nämnas vid namn.

Staffan Ulfstrand fungerade som min handledare från starten. Han tackas varmt, framför allt för det helhjärtade stöd han gav mig och för de många - ibland också mycket långa - diskussioner vi förde.

Ett speciellt tack riktas till Per Brinck för den tålmodighet han visat (t.ex. då jag gång på gång uppskjutit disputationen), och i synnerhet för den förståelse han haft för att min verksamhet som tidskriftsredaktör och barnpassare så allvarligt konkurrerat med avhandlingsarbetet. I detta ljus måste väl också ses att han, trots

byråkratins direktiv, upplåtit arbetsrum och resurser, något som varmt uppskattas.

Skall ytterligare några personer särskilt nämnas, så är det Göran Högstedt, Ulla Holmberg och Johnny Karlsson. Förutom att Göran och jag under årens lopp haft många och åtminstone för mig givande diskussioner, så har han alltid läst manuskript kritiskt och grundligt, vilket resulterat i värdefulla synpunkter. Ulla Holmberg har alltid beredvilligt hjälpt till i institutionens outhärliga bibliotek, vartill hon lika tjänstvilligt som snabbt skaffat fram utlånade böcker och placerat dem på mitt skrivbord. Med Johnny slutligen har jag haft ett givande samarbete, såväl i vetenskapliga som i redaktionella och praktiska angelägenheter. Till de senare räknas byggnadsteknisk rådgivning liksom hjälp vid monteringen av originalen till denna avhandling.

Background and summary of results

Both Great and Blue Tits readily accept nestboxes, and it is therefore hardly surprising that their population ecology has been studied in a large number of places over most of Europe. Kluijver (1951) summarized the results of a study that had continued since 1912. The Dutch study is still going on although in new and more areas. In Oxford, a population breeding in nestboxes on the Wytham estate has been studied from a variety of aspects by David Lack and his co-workers since 1947. Also in other countries have populations of Great and Blue Tits been followed for varying numbers of years, and their breeding biology and population ecology investigated. It is therefore almost certainly true that we have more information about the Great Tit in particular, than we have about any other species of bird, including the Pied Flycatcher. As with every species where we have a great deal of knowledge, puzzling differences between study sites, and numerous contradictory results have been obtained. Some of the major problems with regard to population fluctuations and population regulation that still remain unsolved, and some of the gaps in our knowledge, have recently been well reviewed by Perrins (1980).

This thesis, which is purely empirical, treats various aspects of the breeding biology and population ecology of Great and Blue Tits. Field work was mainly carried out in Linnebjerg, a 24 ha oak wood some 10 km north-east of Lund, southernmost Sweden. This wood was supplied with a large number of nestboxes in the winter 1968/69, and its population of tits followed, with varying intensity, until spring 1978. Problems relating to the regulation of tit numbers, in the strict sense of density dependent influences, will not be treated here. One reason is that some results remain to be analysed; others need to be supplemented with new and extended field experiments before they can provide new information. This applies, for instance, to removal experiments, which I carried out in early spring in several years; at present the results of these experiments merely confirm those obtained in Oxford.

It is, of course, my hope that the eight papers and notes, that comprise this thesis, will add some new information to the one we already have, but also that I have succeeded in pointing out some of the problems and contradictory results that are an unavoidable

effect of so many people working with one or two species. To give but one example, discussed at length in (I). Perrins (1965) found that the probability of survival of fledgling Great Tits was strongly influenced by the date of nest-leaving, broods fledging early having much higher survival rates than broods fledging late. Unless early breeding negatively affects a parent Great Tit's chances to survive to the next breeding season, obviously it would be advantageous to start egg-laying as early as possible. Perrins suggested that Great Tits do not lay earlier than they do because the amount of food available for forming eggs is limiting. A prediction from this hypothesis is that the provision of adequate food should advance laying, a prediction that was supported by my experiments in 1972 and 1973 (II). Yet, in two populations studied, the relation between fledging date and juvenile survival that Perrins found has not been substantiated, rather young from clutches from the middle of the laying period contributed most recruits to following generations. Yet, female Great Tits respond to food supplementation by laying earlier.

In the following paragraphs I will briefly summarize the main results of the papers contained in this thesis.

Part (I) presents basic data on the breeding biology of Great and Blue Tits in Linnebjerg, e.g., start of laying, clutch size, nestling weights, and fledging success. As found in other studies, the start of egg-laying in spring correlated with temperature, being, as expected, earlier in years when temperatures were high. Daily mean temperatures seemed to exert their strongest influence some three weeks before laying started. In the Great Tit, clutch size did not normally decrease with advancing date during the short period during which first clutches were being produced, rather there was some tendency for the very earliest clutches to be smaller than those laid a little later. In some years nestling weights were inversely related to brood size, but the strong positive relationship between nestling weight and subsequent survival that has been demonstrated in the Oxford study was not found; female weight was largely unaffected by nestling number, as was female survival rate; the largest clutches were the most productive, not only to fledging, but also with regard to numbers surviving three months or more. Taken together these observations indicate a strong component of individual adjustment (modification) of clutch size.

Part (II) reports on an experiment where mealworms were supplied to

Great Tits for about three weeks prior to the normal start of egg laying in an attempt to test Perrins' (1965, 1970) hypothesis that female Great Tits start laying as soon as they can gather enough food for forming eggs. The result of the experiment was an advancement of laying by, on average, five days, first year females responding more strongly than older females; later provisioning experiments involving other species of birds have produced similar results, though the amount of advancement achieved has varied. The question whether these results should be accepted as evidence in support of Perrins' food limitation hypothesis is discussed in great length in (I) and in Källander & Karlsson (in manuscript).

At least in the Wytham Great Tit population near Oxford variations in juvenile survival seem to be responsible for the yearly fluctuations in breeding numbers. It has been suggested (Perrins 1965) that the early postfledging period is the critical one, but it has proved difficult to obtain mortality data during this period. In (III) some calculations of postfledging mortality are attempted. Suffering from a lot of uncertainty they nevertheless indicate that mortality, or disappearance, may be considerably higher during the first weeks after nest-leaving than later. Contrary to the convincing results obtained in Oxford, juvenile disappearance rate, as mentioned above, seemed to be unrelated to nestling weight. During the first three weeks after nest-leaving the fledglings had lost on average 1 g compared to their nestling weight on day 15, heavy nestlings losing proportionally more; the reason for the latter result is obscure.

Juveniles start dispersing in early July soon after becoming independent; a second period of increased mobility may take place in September. Whether juvenile dispersal is density dependent or not is not known (but immigration rate may be). Most Great Tits disperse short distances, the vast majority probably settling within 2 km.

The minimum survival rate until November (25 %) was considerably higher than that calculated by Dhondt (1979) for juveniles from the same population in another year.

It is possible that the density dependent migratory movements that are recorded at bird observatories (IV), mainly in October, have a connection with the presumed second dispersal phase in September (see above). At any rate, the numbers of Great Tits recorded on migration or not a linear but an increasing function of population density, which suggest that they might result from interference com-

petition. Availability of beech mast is unlikely to be responsible for the strength of autumn migration, since movements seem to be directly related to density also outside the distribution range of the beech.

As shown in (V) the majority of Great Tits recorded in southernmost Scandinavia in winter originate from South Sweden, the proportion of birds from further north being somewhat higher in the Blue Tit. In the latter species enough recoveries have been made in South Norway to suggest more regular movements of Swedish Blue Tits in a north-westerly direction. Some Great Tits caught in South and South Central Sweden in winter have later been found in the far north (several of them in winter); but at present the Swedish ringing material is too scanty to provide a more detailed picture of the movements undertaken by tit populations in different parts of the country.

Hard winters have often been shown to have a strong negative effect on the size of resident bird populations, but correlations between winter temperatures and breeding numbers of tits in Wytham have not shown any relationship between the two (Perrins 1980). From the results presented in (VI) I conclude that there is a clear positive relationship between winter temperatures and the subsequent breeding density of several species of birds, Great and Blue Tits included, in more northerly and more continental areas, respectively. The population size of the two tit species, and that of the Nuthatch, were also positively related to the size of the beech mast crop in the preceding autumn.

Winter temperatures no doubt act through their effects on energy requirements and food availability. Therefore, winter feeding should result in increased survival (VII). This was supported for the Great Tit in one of two winters, but not in the Blue Tit. After the second winter both experimental and control populations of the Great Tit increased; it was suggested that this was an effect of a rich beech mast crop in that winter. It should be pointed out here that, because it is so densely populated, SW Skåne is not an ideal area for carrying out this kind of experiment. Tits are known to fly considerable distances to feed at human habitations when conditions are severe. An illustration of this was obtained in winter 1981/82 when flocks of Great Tits were seen leaving the wood Dalby Söderskog at dawn for

the gardens of the village Dalby only to return at dusk to roost in the wood.

In the final note (VIII) I test whether divorcing pairs of the Great Tit, i.e. pairs that had bred together and subsequently mated with a new partner despite their former mate being alive, thereby increased their fitness. I also test whether adult birds tended to mate with other adults, as might be predicted from the results of Harvey et al. (1979). There was some indication that females increased their production of fledglings after a divorce, while the reverse was true for males; poor breeding success was however not the reason why about a third of the pairs divorced between two breeding seasons. There was no bias in mating frequencies when adults that remained together were excluded from the comparison.

REFERENCES

- Dhondt, A.A. 1979. Summer dispersal and survival of juvenile Great Tits in southern Sweden. Oecologia 42: 139-157.
- Harvey, P.J., Greenwood, P.J., Perrins, C.M. & Martin, A.R. 1979. Breeding success of Great Tits Parus major in relation to age of male and female parent. Ibis 121: 216-219.
- Källander, H. & Karlsson, J. In manuscript. Laying date and breeding performance in the Starling Sturnus vulgaris: effects of supplemental food.
- Kluijver, H.N. 1951. The population ecology of the Great Tit Parus m. major L. Ardea 39: 1-135.
- Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus major. J. Anim. Ecol. 34: 601-647.
- Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.
- Perrins, C.M. 1980. Survival of young Great Tits, Parus major. Acta XVII Congr. Int. Orn. Berlin: 159-174.

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1. INTRODUCTION

1.1 Study area, population

Linnebjerg (55°44'N, 13°18'E) is a nature reserve with mature oak wood, 23.8 ha in size and only lightly managed, surrounded on all sides by agricultural land and pastures. Quercus robur L. strongly dominates the tree stratum with Tilia cordata Mill. the second commonest tree (approx. 20 %). A block of less than 1 ha is pure Fagus sylvatica L., while small patches and scattered trees of Populus tremula L., Betula verrucosa Ehrh., Prunus avium L., and Sorbus aucuparia L. occur throughout the wood. In most parts the canopy is almost closed, but nearly 1 ha is occupied by an open luxurious meadow with tall forbes, scattered bushes, and a few trees; other small openings are found in several places. The understory is strongly dominated by Corylus avellana L., reaching about 5 to 6 m in height. Sambucus racemosa L. is fairly common in some parts, Crataegus is an important element throughout the wood, whereas Viburnum opulus L. occurs here and there in the openings. The ground vegetation shows a typical seasonal succession with an almost pure cover of Anemone nemorosa L. in early spring, later followed by an almost equally pure cover of Convallaria majalis L., finally to be replaced by forbes such as Melandrium rubrum Garcke and Aegopodium podagraria L. In late summer and autumn large parts of the wood are more or less devoid of forbes.

About 160 nestboxes were used in 1969 to 1973 giving an average density of 6.7 boxes ha⁻¹; an additional 20 were put up in 1974, supplemented with a further 30 in 1975. These were erected in part of the wood only, in order to test the influence of nestbox density on the breeding density of the tits. Nestbox density in the experimental part rose to approximately 16 ha⁻¹, but the tits did not breed at higher density in the densely boxed area than in the rest of the wood.

The numbers of breeding pairs of Great Tits Parus major and of Blue Tits P. caeruleus, and of Pied Flycatchers Ficedula hypoleuca are given in Tab. 1; other species used the boxes only rarely, e.g. Nuthatch Sitta europaea four times and Robin Erithacus rubecula once; thus, in every year a substantial proportion of the boxes remained unoccupied. Mixed clutches of Great and Blue Tits were, however, found twice (Källander 1980).

No Great Tit nests were found in natural holes within Linne-

Tab. 1. The number of pairs of Great Tit *Parus major*, Blue Tit *P. caeruleus*, and Pied Flycatcher *Ficedula hypoleuca* breeding in nestboxes in Linnebjerg in 1969 to 1978.

	Great Tit	Blue Tit	Pied Flycatcher
1969	19	5	c. 19
1970	30	6	23
1971	46	10	31
1972	58	13	26
1973	68	16	31
1974	51	9	45
1975	46	19	c. 25
1976	23	14	c. 25
1977	60	13	c. 29
1978	31	5	c. 30

bjer, but in 1970 a known female raised a brood in an oak tree just outside the wood. In all probability all Great Tits inside the wood nested in the boxes, because in 1973 and 1974, Great Tit territories were mapped in spring, and all individually identifiable males (94 %) except one (who held a small territory for only a few days) could later be connected with a box containing a nest. An unknown number of Blue Tits bred in natural holes each year. Although Blue Tit territories were never mapped, it was obvious from several kinds of information that Great Tits strongly outnumbered Blue Tits in Linnebjerg. This is contrary to the situation on the Continent and in England, where the proportions of the two species in oak wood are either more similar (e.g. Sasvari 1975), or the Blue Tit dominates (e.g. Campbell 1968, Belman 1980).

Simple wooden boxes with a bottom area of 10 by 12.5 cm and a 35 mm entrance hole were used. They were fairly evenly distributed throughout the wood at heights between 1.5 and 3.5 m. During the reproduction period they were usually inspected about every 5 day, less regularly later in the season, which lead to a missing of accurate data on clutch size for second clutches in some years. In 1969, inspections were incomplete and data on clutch size are largely missing; in 1975, the fate of most broods is unknown; in 1976, no inspections were carried out after clutch size had been determined.

The date of laying of the first egg was calculated assuming the laying of one egg a day, which, of course, may introduce a small

error in some years. The young were ringed and weighed on their 15th day. In most cases I did not visit the nest on the day of hatching and so hatching date had to be determined from the developmental stage of the nestlings on later visits. Hatching is not perfectly synchronous even in first clutches (Neub 1979). Both factors may have influenced the variance of the weighing data.

During the first years of the study both males and females were caught in the boxes when feeding young; for the next years most Great Tits were colour ringed and males checked on their territories, while females were taken at night when they slept in their boxes together with the nestlings. The proportion of ringed males decreased over the years and most information therefore refers to females which were controlled each year until 1976. Few male Blue Tits were ringed, but most females that bred in boxes were.

Some set of data was missing for a few clutches each year, which explains the discrepancies in sample size between, e.g., the number of clutches and number of broods presented in the tables.

1.2 Desertions, predation, and egg losses

1.2.1 Great Tit

Of 378 first clutches, only four (1.1 %) were deserted during the incubation stage (one having failed to hatch after 1 month of incubation. Two out of 29 (7 %) of the second clutches were deserted during laying or incubation.

No predation took place during the egg stage (apart from a partial loss mentioned below) except that, in 1969, before a metal shielding was applied around the entrance hole, two boxes were severely damaged by Red Squirrels Sciurus vulgaris L. resulting in loss of the clutches. There was, however, more often than not a certain discrepancy between the number of eggs laid and the number of young fledged. This is explained by eggs failing to hatch and by young dying in the nest; mostly the fate of the missing nestlings could not be ascertained. Some of the losses might have been caused by Great Spotted Woodpeckers Dendrocopos major (L.) reaching down for young through the entrance hole, but only once was one observed attempting this.

1.2.2 Blue Tit

The Blue Tit had a slightly higher rate of desertion. Three completed or probably completed first clutches out of 66 started (4.5 %) and one of four second clutches was deserted during laying.

As in the Great Tit, no predation took place during the egg stage, and losses in the nest were either due to eggs failing to hatch or to young disappearing.

2. BREEDING PHENOLOGY

2.1 Start of laying: older vs 1-y old females

2.1.1 Great Tit

Older females of the Great Tit tend to start laying a few days earlier than 1-y females (e.g., Perrins 1965). This was tested for the years 1970 to 1975, when most females were ringed and their age known. Every spring there was a proportion of unringed females (immigrants) in the breeding population. Since older females are known to be highly sedentary (Harvey et al. 1979, and others) immigrant females were assumed to be 1-y old.

Older females started laying earlier than 1-y females in four of the six years: in 1970 (2.6 d), 1972 (2.0 d), 1973 (4.7 d), and 1975 (3.4 d), based on arithmetic means. Differences in median laying dates were statistically significant in 1972, 1973, and 1975, but not in the other three years (median test, χ^2). In these calculations I excluded birds subjected to the provision of mealworms in an experiment aimed at elucidating the role of food availability in determining the onset of laying (Källander 1974). Tab. 2 summarizes the timing of laying by different female age classes in relation to the population as a whole.

2.1.2 Blue Tit

In 20 cases where female age was known, as in the Great Tit, older females showed a tendency towards laying earlier than 1-y old females (Källander 1976).

2.2 Start of laying: in relation to female weight

Jones (1973) found a positive correlation between the start of laying in the Great Tit and the weight of the female in the pre-

Tab. 2. Number of female Great Tits Parus major of different age classes starting egg laying before and after the median date for the population, years 1970 to 1975 combined (birds laying on median date excluded).

	Age of female			
	1y	2y	3y	>4y
Before median	47	32	14	3
After median	67	13	4	5

Note: difference between 1y old and older females significant at $p < 0.001$, between 1y and 2y females at $p < 0.01$, and between 1y and 3y old females at $p < 0.001$ (median test, χ^2); differences between older age classes not statistically significant.

ceding winter, 1 g increase in weights corresponding to a delay of egg-laying by 2 days. Weights were found to be remarkably constant during the winter and consequently more reliable than those obtained during the breeding period when females increase in weight in connection with egg-formation (Kluijver 1952) and decrease in the course of incubation (van Balen 1973); during the nestling phase their weights may, as shown below (section 5.3.5), vary with the number of young in the nest. Because winter

Tab. 3. Median date for the laying of the first egg in first clutches of the Great Tit Parus major and the Blue Tit P. caeruleus in 1970 to 1978, together with data on range and on proportion of clutches started in April in each year. N = No. of clutches on which median is based. All Great Tit clutches that were subjected to experimental advancement of laying in 1972 and 1973 were omitted.

Year	Great Tit				Blue Tit			
	Median date	No. of days between the start of 1st and last clutch	% clutches started in April	N	Median date	No. of days between the start of 1st and last clutch	% clutches started in April	N
1970	9 May	16	0	30	9 May	6	0	5
1971	11 May	9	2.2	46	10 May	15	0	10
1972	6 May	22	3.0	33	5 May	13	21.4	14
1973	10 May	19	0	43	6 May	8	0	16
1974	8 May	24	28.3	46	24 Apr	23	62.5	8
1975	11 May	18	2.2	45	10 May	11	0	18
1976	11 May	10	0	22	(14 May	3	0	(2)
1977	5 May	14	1.7	59	4 May	12	15.4	13
1978	13 May	13	0	18	-	-	-	-

weights showed little variation and all birds caught appeared well fed, Jones concluded that the weights probably reflected body size (rather than amounts of fat stored).

In the winters of 1972 and 1973, I mist-netted and weighed a large number of Great Tits. Since many of them were later found breeding, the winter weights of the females could be correlated with laying dates in the following spring. Due to the mealworm experiment mentioned above, experimental and control birds had to be analysed separately in 1973, which reduced sample size, but the number of females was adequate in both years. Yet no statistically significant correlation emerged. This may have been either because no relation exists between weight and laying date, or because winter weights were too variable at Linnebjerg to reveal it. Winter weights are known to vary inversely with ambient temperature (Owen 1954), and temperatures did vary considerably over the period that tits were caught.

2.3 Start of laying: differences between years

2.3.1 Great Tit

Tab. 3 gives the median date for the laying of the first egg of first clutches in each year 1970 to 1978. In every year, half the population had started laying in the first or second week of May. The largest difference between any two of the years was only 8 days. The earliest dates on which clutches were started (excepting those subjected to the feeding experiment mentioned above) were 21 April 1972 and 23 April 1974, and the latest dates were 19 May 1973 and 20 May 1978.

1974 differed in two respects. First, egg-laying commenced already in April in a larger number of nests than in any of the other years (Tab. 3). Second, laying was rather irregular, being interrupted for at least 1-5 days in 8 early nests. Most probably the irregularities can be explained by temperature variations during the last week of April. At Lund, the mean for the whole month was more than 1°C above normal. On the 24th, however, there was a sudden drop in temperature, and temperatures well below freezing were recorded during two successive nights. As the boxes were not checked daily, it is unfortunately not possible to determine the precise relation between the interruptions in laying and the drop in temperature.

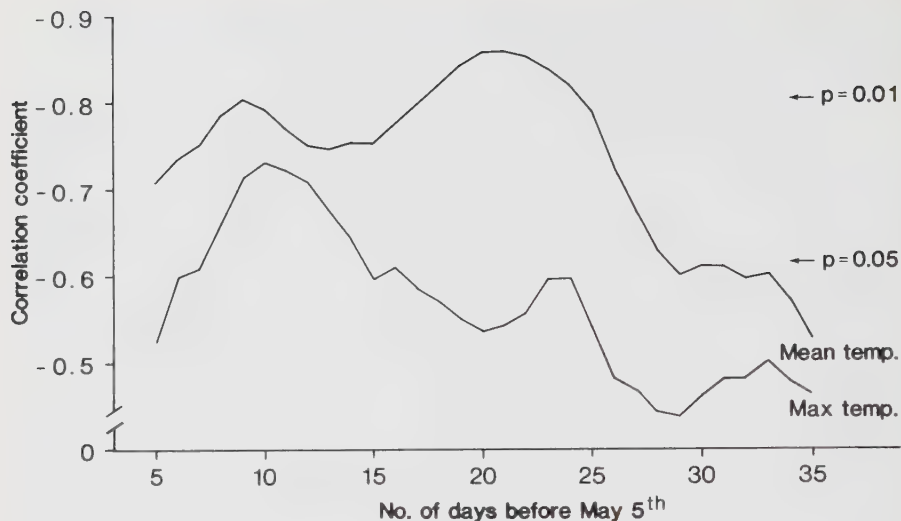


Fig. 1. Changes in the strength of the correlation between warmth sums (see text) and the mean laying date of Great Tits in Linnebjerg as a function of the length of period over which temperatures are summed. The upper curve gives the correlation coefficients for the relation between daily mean temperatures and laying date, the lower curve that between daily maximum temperatures and laying date. Mean temperatures seem to exert their strongest influence about 3-4 weeks before laying starts, while maximum temperatures have in influence much later.

Various authors have correlated the start of egg-laying with warmth sums, i.e. daily temperatures cumulated over a specified period prior to laying (e.g., Kluijver 1952, Perrins 1965, 1973, Fredriksen et al. 1972, Jones 1973). This has been done either by using fixed calendar dates or by adjusting the period to the observed laying dates (by, for instance, considering all dates up to four days before the first egg is laid). Generally a good agreement has been found between warmth sums and laying dates. However, the length of the temperature period influencing the onset of laying seems to decrease with latitude (Slagsvold 1976). Here I used a fixed ending date (5 May) and correlated the mean laying dates with warmth sums for successively longer periods. The highest correlation coefficients were obtained for a period starting in mid-April, i.e. roughly three weeks before the normal start of egg-laying, and with daily mean temperatures; daily maximum temperatures gave much lower correlation coefficients (Fig. 1). Thus it seems as if the start of laying at Lund is in-

fluenced by temperatures during a much shorter and later period than is the case in Britain and on the Continent, in agreement with Slagsvold's (1976) suggestion.

2.3.2 Blue Tit

Tab. 3 presents median laying dates for the years 1970 to 1977. The table includes data from 7 and 3 clutches, respectively, laid in those parts of the wood where mealworms were supplied in 1972 and 1973 (see above). Although there was a tendency for Blue Tits within those parts to start earlier ($0.1 > p > 0.05$; median test χ^2), suggesting that also the Blue Tits were affected by the availability of extra food, their inclusion does not alter the result that, in most years, the Blue Tits started laying slightly earlier than the Great Tits, which is the pattern normally found (references in Perrins 1979).

One year, 1974, was quite exceptional in that 5 out of 8 clutches were started before 26 April, the first egg being laid already on the 20th, the earliest starting date recorded in any of the years (Tab. 3). Contrary to the case in the Great Tit, laying was regular (1 egg each day) also in clutches started in April.

3. CLUTCH SIZE, FIRST CLUTCHES

3.1 In different years

Tab. 4 gives the clutch size distribution in each year 1970 to

Tab. 4. Clutch size distribution among first clutches of the Great Tit Parus major in 1970 to 1978.

Year	Clutch size											$\bar{x}$	SD	N	
	4	5	6	7	8	9	10	11	12	13	14				
1970		1	1	3	6	6	10	2					8.83	1.46	29
1971				1	4	5	11	16	5	3			10.42	1.39	45
1972				2	9	9	22	11	1	1			9.69	1.23	55
1973		1	4	6	11	14	18	9	1				9.00	1.54	64
1974	1	1	2	2	5	11	10	7	3	2			9.39	1.94	44
1975		2		5	8	14	9	5	3				9.06	1.59	47
1976					1	5	2	8	4	2			10.68	1.39	22
1977					5	10	14	16	11	3			10.46	1.34	59
1978					2	2	5	6	2	5	2		11.13	1.75	24

1978 for the Great Tit, and tab. 5 summarizes that of the Blue Tit in each year 1970 to 1977.

Tab. 5. Clutch size distribution among first clutches of the Blue Tit Parus caeruleus in 1970 to 1978.

Year	Clutch size								$\bar{x}$	SD	N
	8	9	10	11	12	13	14	15			
1970			1	2		2	1		12.00	1.55	6
1971		1		1	4		4		12.40	1.65	10
1972				2	3	4	4		12.77	1.09	13
1973				3	4	6	1	1	12.53	1.17	15
1974	3		1	1	1	1			10.00	2.08	7
1975			7	2	2	6			11.41	1.37	17
1976			1		1				11.00		2
1977				2	1	8	1		12.67	0.93	12

Tab. 6. Mean clutch size of 1year old and older female Great Tits Parus major in 1970 to 1976. Differences tested with Student's t-test.

Year	1year old females			Older females			Difference	Sign. level p
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N		
1970	8.55	1.61	20	9.50	0.93	8	0.95	0.13
1971	10.21	1.37	34	11.09	1.30	11	0.88	0.066
1972	9.14	1.13	29	10.32	1.07	25	1.18	0.0002
1973	8.50	1.65	32	9.59	1.24	29	1.09	0.005
1974	8.74	2.07	24	10.20	1.43	20	1.49	0.009
1975	8.80	1.66	25	9.26	1.59	19	0.46	0.356
1976	10.29	1.38	14	11.37	1.88	8	1.08	0.076

Tab. 7. Number of Great Tit Parus major females in each age category laying a clutch larger or smaller than the year's median clutch size (clutches of median size excluded), years 1970 to 1975.

	Age of female (years)			
	1	2	3	≥ 4
Clutch > median	43	26	14	6
Clutch < median	81	13	8	5

3.2 In older and 1-y old females

3.2.1 Great Tit

On average older females lay larger clutches than 1-y old females (e.g., Perrins 1979). This was true also in the present study. In all years, older females had a mean clutch size between 0.46 and 1.49 eggs larger than had 1-y old females, the difference being statistically significant or nearly so in 5 out of 7 years (Tab. 6).

Although an analysis showed females 3 y old or more to lay a clutch on average 0.5 eggs smaller than that of 2-y old females, the proportion of clutches laid by these two categories of females that were larger and smaller, respectively, than the population's median clutch size did not differ (Tab. 7).

3.2.2 Blue Tit

There was no difference in clutch size between older and 1-y old females in 25 cases where female age was known (Källander 1976).

3.3 In relation to date of laying

3.3.1 Great Tit

Clutch size in the Great Tit tends to be larger earlier in the season than later (references in Perrins 1979) as is the case in many other temperate zone passerines (Klomp 1970). This decrease with season has been reported both in comparisons between years and within a single year (Kluijver 1951, Lack 1958).

During 1970 to 1978, there was no obvious correlation between mean clutch size and median (or mean) laying date in Linnebjerg (Fig. 2), but clutch size is known to vary negatively with popu-

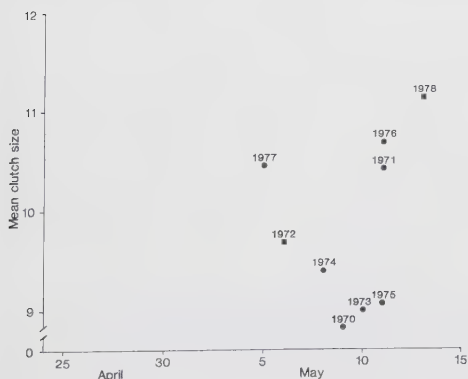


Fig. 2. Mean clutch size of the Great Tit in Linnebjerg in relation to median laying date.

lation density (e.g., Perrins 1979). However, no effect of laying date on clutch size was found when population density was kept constant.

As mentioned above, all genuine first clutches were started within a comparably short period of time each year (Tab. 3). Within that time span there was a statistically significant decrease in clutch size only in 1978, and an almost significant one in 1974 ($p < 0.01$ and $0.1 > p > 0.05$, respectively; linear regression of clutch size on laying date, data available for 9 years). In 5 years the slope of the regression line had a positive sign (but mostly close to zero).

3.3.2 Blue Tit

In the Blue Tit, contrary to the situation in the Great Tit, there seemed to exist a negative correlation between the mean clutch size and the median laying date of the population, ($r_s = 0.93$, $p < 0.01$, one-tailed), clutch size decreasing by approximately 0.15 eggs d^{-1} , if one excludes 1974 (Fig. 3). That year, however, was quite exceptional in that the very early median date (25 April) was associated with the lowest mean clutch size during the study (10.0 eggs).

Within the compressed laying period of the first clutches (Tab. 3), clutch size did not decrease significantly with date in any single year. When, however, the difference in size of each clutch from the year's mean was plotted against the corresponding deviation in laying date from the year's median, for all years combined, a statistically significant decrease of about 0.1 egg d^{-1} resulted ($r = 0.41$, $p < 0.001$).

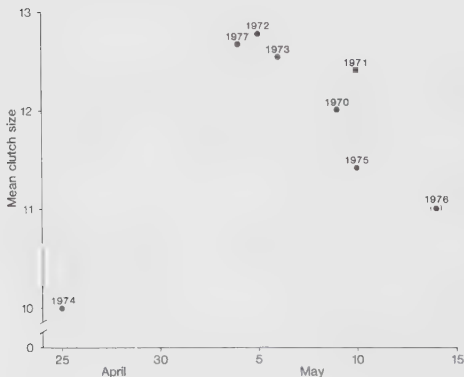


Fig. 3. Mean clutch size of the Blue Tit in Linnebjerg in relation to median laying date.

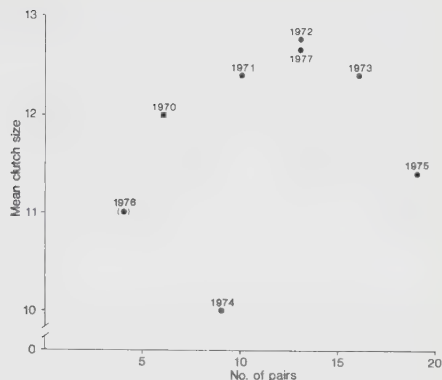
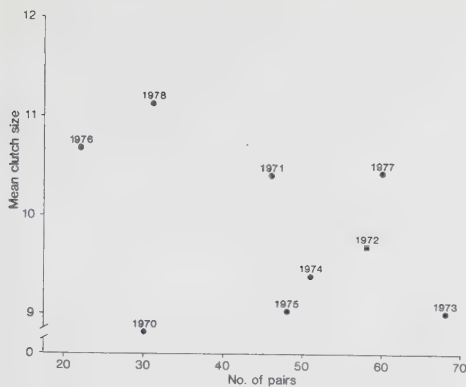


Fig. 4. Mean clutch of the Great Tit in Linnebjerg in relation to population density.

Fig. 5. Mean clutch size of the Blue Tit in Linnebjerg in relation to population density (as reflected by the number of pairs breeding in the nestboxes).

3.4 In relation to population density

3.4.1 Great Tit

The expected negative correlation between mean clutch size and population density (e.g., Perrins 1979) is far from statistically significant (Fig. 4), and the same is true when corrected for the influence of laying date.

3.4.2 Blue Tit

There was a weak (although not statistically significant) tendency for clutch size to vary positively with the number of breeding pairs (Fig. 5).

4. SECOND CLUTCHES

4.1 Frequency in relation to population density

The proportion of second clutches is known for 7 years in the Great Tit and tended to vary negatively with population density (Tab. 8); in the Blue Tit second clutches only occurred in 1969 (5 first clutches and 4 second clutches).

4.2 Frequency in relation to date for the first clutches

The proportion of second clutches in the Great Tit did not vary with the median laying date of the population's first clutches,

Tab. 8. Proportion of second clutches in relation to number of breeding pairs of Great Tits Parus major.

Year	1969	1970	1974	1977	1972	1973	1971
No. of pairs	19	30	51	60	58	68	46
% 2nd clutches	42	40	10	10	7	1	0

but the timing of the individual female's first clutch influenced the probability of her laying a second clutch. Thus, of 18 known females laying second clutches, 15 had started their first clutch before the median date of the population against only 3 after ($p = 0.008$, binominal test). There was no tendency for older females to start second clutches more often than for 1 y old females to do so.

4.3 In relation to number of young fledging from first brood

Those Great Tit females that started second clutches in 1969 and 1970 fledged fewer young from their first broods than did those that did not lay second clutches (means 4.86 and 4.45 against 7.64 and 7.79, respectively; differences statistically significant: $p < 0.05$ and 0.01 ; t-test).

The mean weights of the two categories of females also differed (weighed when feeding first brood young); the females starting second clutches in 1969 weighed 20.09 g (S.D. 1.46) against 18.64 g (S.D. 0.96) for those not having a second clutch ($p < 0.05$, t-test). In 1970, the corresponding weights were 19.04 (S.D. 0.92) and 18.05 (S.D. 0.76) ($p < 0.01$, t-test).

4.4 Clutch size of second clutches

Mean size of second clutches in the Great Tit was 7.26 (S.D. 5.63, $n = 19$), i.e. considerably lower than for first clutches (that of the few Blue Tits is not known).

4.5 Clutch size of second clutches in relation to laying date

Contrary to the case with first clutches of the Great Tit in most years, there was a statistically significant decrease in the size of second clutches with advancing date for their start (by 0.4 eggs d^{-1} ; $r = 0.797$, $p < 0.001$).

4.6 Overlap between first broods and second clutches

In 8 out of 18 second clutches in 1969 and 1970, where the identity of the female could be determined, the laying of the second clutch started while the young of the first brood were still in the nest; in another 6 cases nest building must have taken place (in one or two of these possibly also laying).

5. NESTLING WEIGHT

Perrins (1965) found that nestling weight on the 15th day decreased with increasing brood size and with the progress of the season (although the form of the latter relationship was quite variable), and that the nestlings' weight affected their chances of later being retrapped locally; more heavy than light young were controlled 3 months or more after fledging. In 1969 to 1974, I weighed nearly all nestlings on their 15th day when they have usually attained full nestling weight (Neub 1979) and the risk of causing premature leaving is minimal. All nestling weights discussed below refer to this age.

5.1 In relation to brood size

5.1.1 Great Tit

Mean nestling weight of first broods decreased by 0.11 to 0.16 g for each additional nestling in the brood in 1969 to 1972 but only by 0.03 and 0.04 in 1973 and 1974 (linear regressions of mean nestling weight on brood size). The negative correlation between nestling weight and brood size was statistically significant only in 1969 and 1971 ($p < 0.02$ and 0.01 , respectively) but almost so in 1970 and 1972 ($0.1 > p > 0.05$).

5.1.2 Blue Tit

In the Blue Tit, no differences in mean nestling weight were found for brood sizes 8 to 14 young.

5.2 In relation to hatching date

5.2.1 Great Tit

Fig. 6 presents mean nestling weight for each brood that was weighed in the years 1969 to 1974. A correction for the influence of brood size does not alter the general picture.

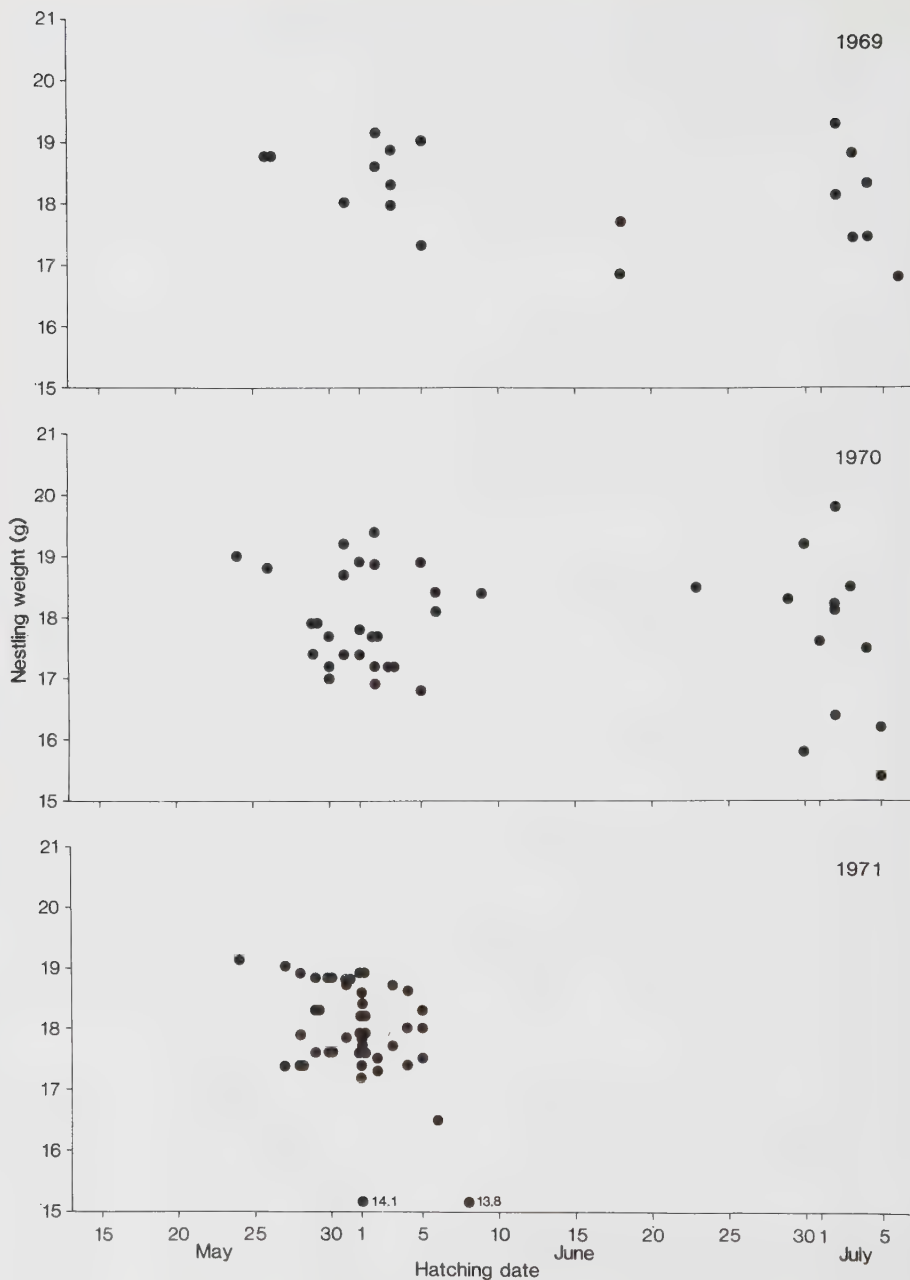
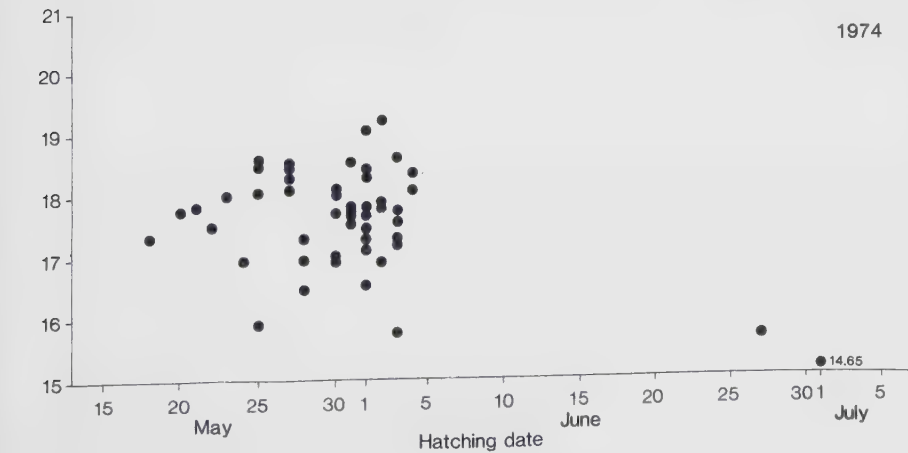
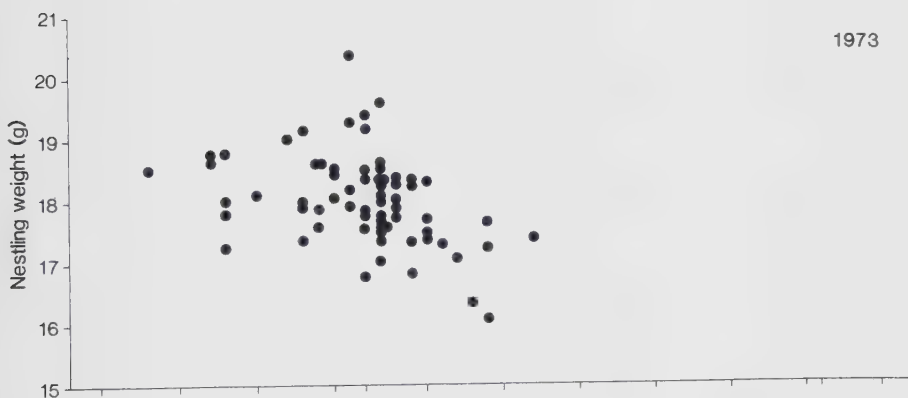
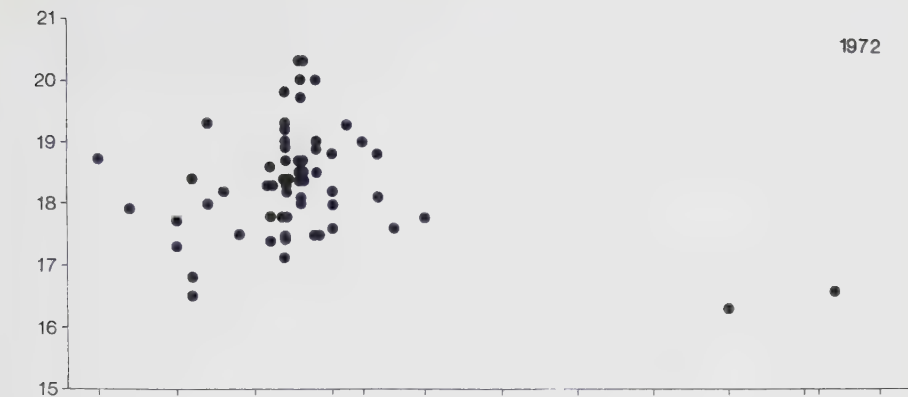


Fig. 6. Nestling weights of Great Tits in Linnebjerg in 1969-1974 in relation to season. Each dot represents the mean weight of the young of a brood plotted against the hatching date of that brood.



In 1969 and 1970 brood weights tended to be high and fairly constant over much of the breeding season including those of the fairly numerous second broods. The low weights of the very last second broods to hatch, however, suggest a steep decline with date which was also found in other deciduous woods (Källander in manuscript). In 1971, weights were high over the compressed breeding period with the exception of two broods of extremely low weights hatched on 1 and 8 June, respectively. The reason for their strikingly low weights is unknown. Although some rain had fallen on the days preceding their weighing, bad weather does not seem to be an adequate explanation, at least not for the earlier one, because other broods that hatched on the same day or later were of normal weight. The death of the male parent is one possibility. However, in 1971, mean nestling weight decreased with date in two other woods, and in one of them several broods that hatched about 1 June had mean weights below 15 g (Källander in manuscript). In 1972 to 1974, there was a tendency for weights to show a peak (reached by birds hatched on 28 May 1972, 31 May 1973, and 2 June 1974); the mean weights of birds that hatched earlier tending to increase with date, those of birds that hatched later tending to decrease. In 1974, this decrease was statistically significant for birds that hatched after 1 June ($r = -0.549$, $p < 0.01$; linear regression of mean weights on date). Although food abundance was not measured, I noticed that caterpillars, which had been extremely numerous earlier that year, suddenly disappeared by mid-June coincident with the decrease in mean nestling weights.

5.2.2 Blue Tit

In this species, no decrease in mean brood weights was observed over the short period that first broods were found in the boxes.

5.3 In different years

Mean nestling weight of first brood Great Tits varied between 17.71 g in 1974 and 18.33 g in 1972, i.e. a difference of 0.6 g. Young in 1972 were heavier than young in 1971, 1973, and 1974, and young in 1973 were heavier than young in 1974 (t-test). Apart from these, differences were not statistically significant. Mean weights and the mean number of young fledging in each year did not correlate. Although females were heaviest in the two years

when mean nestling weights were highest, this correlation did not hold for the other four years.

6. FLEDGING SUCCESS

6.1 First broods

6.1.1 Great Tit

Tab. 9 gives the number of fledged young from first broods in 1969 to 1974 and in 1977 (including only clutches where eggs hatched). The mean number of young fledged varied between 6.35 in 1970 and 8.91 in 1977.

Tab. 9. Number of young of the Great Tit Parus major fledging from first clutches that hatched, years 1969 to 1974, and 1977.

Year	No. of young fledging from nest													$\bar{x}$	S.D.	N	
	0	1	2	3	4	5	6	7	8	9	10	11	12				13
1969			3		2	2		2	4	4			1		6.56	2.89	18
1970	2	1	2	3	1	2	3	7	1	4	3	1			6.00	3.12	30
1971						1		6	8	6	16	5	3	1	9.33	1.65	46
1972			1					2	5	15	13	15	6	1	8.86	1.62	58
1973					4	3	6	12	10	16	11	4	1		8.07	1.90	67
1974			2	1	3	3	3	5	7	13	9	3			7.82	2.34	49
1977			1	1	2	2	3	4	4	16	8	11	3	2	8.91	2.41	57

Between 72 and 91 % of the eggs that hatched resulted in fledged young. The proportion of losses due to eggs failing to hatch varied between 2.6 and 7.9 %, while nestling disappearance varied between 5.5 and 11.4 % (Tab. 12). In nearly 80 % of the nests all eggs hatched, in about 12 % of the nests 1 egg failed to hatch, in about 3 % 2 eggs, in about 2 % each 3 and 4, and in about 1 % more than 4 eggs did so; partial hatching failure was not related to clutch size. Nestling disappearance was similarly distributed although with a lower proportion of nests without losses (60 %); 1 young was lost in 25 %, 2 in about 7 %, 3 in about 4 %, and more than 3 in about 3 % of the broods.

Tab. 10. Disappearance of nestling Great Tits Parus major from first broods of different initial brood size (data from 1971 to 1974).

	Initial brood size							
	1 to 6	7	8	9	10	11	12	13
% disappearing	5.1	5.4	3.9	5.2	6.7	6.6	10.5	13.5
Total No. of young in each brood size	99	112	256	405	510	407	84	52

Nestling loss increased non-linearly with brood size (Tab. 10), but nevertheless more young fledged the larger the initial brood (or clutch) size, i.e. within the range observed, the largest clutch sizes were also the most productive (to the point of fledging).

6.1.2 Blue Tit

The mean number of young fledging from clutches that hatched varied between 8.25 in 1969 and 11.70 in 1971 (Tab. 11), showing some correlation with the fledging rate of the Great Tit ($p < 0.05$; Spearman rank, one-tailed).

Whereas nestling losses were fairly similar in different years, the proportion of unhatched eggs varied between years (Tab. 12), but this is probably an effect of small sample size; the higher proportion in 1973 and 1977 was due to 3 clutches where 4 to 5 eggs failed to hatch. In 65 % of the nests all eggs hatched; in 24 % 1 egg, and in 11 % 2 to 5 eggs failed to hatch. As in the Great Tit, partial hatching failure showed no relation to clutch size. Nestling losses were very similar: 58 % of the nests suffered no losses, 28 % lost 1 nestling, 8 % lost 2, and 6 % lost 3. Contrary to the case in the Great Tit, there was no tendency for nestling losses to increase with initial brood size.

6.2 Second broods

Although clutch size was lower in second than in first clutches of the Great Tit, second broods suffered heavier losses, less than 70 % of the eggs laid resulting in fledged young in 1969 to 1972. In 1974, the 3 clutches that hatched, produced only 5 fledged young altogether (and another 2 clutches were deserted at the egg stage).

Tab. 11. Number of young of the Blue Tit Parus caeruleus fledging from first clutches that hatched, years 1969 to 1964, and 1977.

Year	No. of young fledging from nest									$\bar{x}$	S.D.	N
	6	7	8	9	10	11	12	13	14			
1969	2			1			1			8.25	2.87	4
1970			1	1	1		2	1		10.67	1.97	6
1971			1			3	4		2	11.70	1.70	10
1972			1	1		4	2	3	2	11.69	1.80	13
1973	1				6	2	3	3		10.87	1.81	15
1974	1		3	1	2		2			9.22	1.99	9
1977	1		2				3	5		11.18	2.56	11

Tab. 12. Nest losses, expressed as a percentage of eggs laid, in the Great Tit Parus major and the Blue Tit P. caeruleus, years 1970 to 1974, and 1977.

Year	Great Tit			Blue Tit		
	Unhatched eggs	Nestling losses	Total losses	Unhatched eggs	Nestling losses	Total losses
1970	?	?	28.1	?	?	11.2
1971	2.6	7.9	10.5	1.6	4.0	5.6
1972	2.8	5.8	8.6	2.6	5.2	7.8
1973	4.7	5.5	10.2	8.5	3.7	12.2
1974	7.9	8.8	16.7	0	5.7	5.7

1977	3.4	11.4	14.8	8.5	4.3	12.8

In the Blue Tit, the 3 second clutches that hatched in 1969 resulted in 6, 6, and 7 fledged young, respectively, while a fourth clutch was deserted at the egg stage (cf. Tab. 11).

6.3 In relation to time of year

The number of Great Tits fledging from each brood in relation to its hatching date is shown for the years 1969 to 1974 in Fig. 7. In 1969, 1970, and 1973, fledging success was lower for the very earliest broods, increasing towards the mean hatching date for the population. Also Vilbaste (1982) found that the earliest broods sometimes had a very low productivity. The low, and steeply declining, fledging success of second broods is also clearly seen.

6.4 In relation to the age of the female

The mean difference between the number of eggs laid and the number of young fledging from first clutches of the Great Tit was 1.01 ($n = 142$) for 1 y old females, 0.92 ($n = 46$) for 2 y old females, and 1.67 ($n = 36$) for females 3 y old or more. Thus, disregarding the fact that 2 y old females started off with a clutch on average 1 egg larger than did 1 y old females, there was no difference between these categories of females in their ability to raise young, whereas females 3 y old or more suffered greater losses. There was, however, a difference between 1 y old and older females with respect to when large nest losses took place (large losses here defined as more than 30 % of the eggs laid failing to hatch or more than 30 % of the hatchlings disappearing. Whereas large losses of young fell fairly evenly on the two categories of females (8.6 and 11.8 % of the nests, respectively), a large proportion of unhatched eggs was found in only about 1.5 % of the nests of 1 y old females against in 11 % of those of older females. This may indicate that older females were more susceptible to the disturbance caused by nestbox inspections during the incubation phase.

7. RETRAPS OF BIRDS RINGED AS NESTLINGS

Perrins (1965) found that usually more young from early than from late, and more young from heavy than from light broods of the Great Tit were still present in his study area 3 months or more after fledging. No tits were mist-netted in Linnebjerg in the first winters, so in these years retraps refer to birds that subsequently bred. From the winter 1971-72 onwards tits were mist-netted in winter and so birds controlled in this way could be included in the analysis.

7.1 In relation to date of hatching

7.1.1 Great Tit

As mentioned above, late broods were few in most years. However, I divided each breeding season into four periods, calculated the number of young fledged within each of them, and compared the number of young from each period subsequently controlled more than 3 months later with the number expected on equal chances of recovery. Statistically significant deviations from the expected values were found only in 1969 and 1970 ($p < 0.02$ in both years;

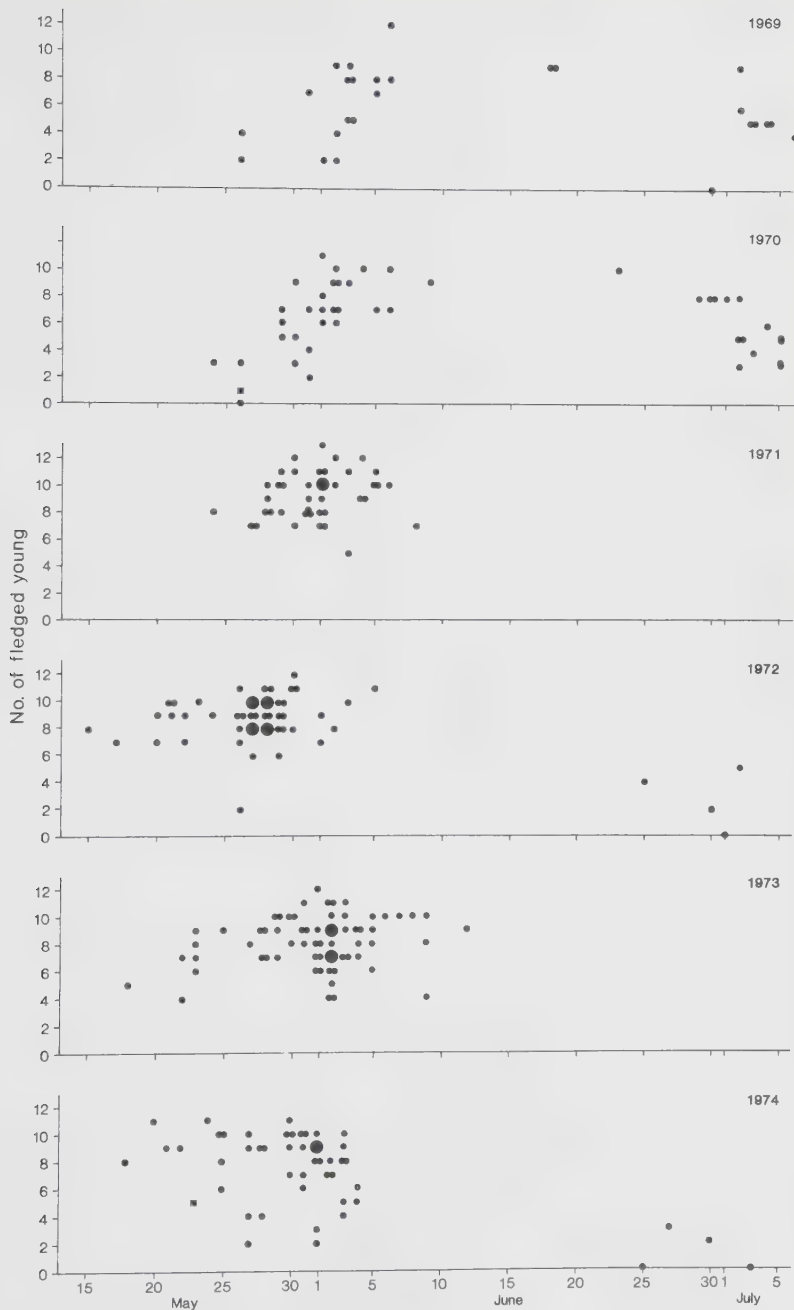
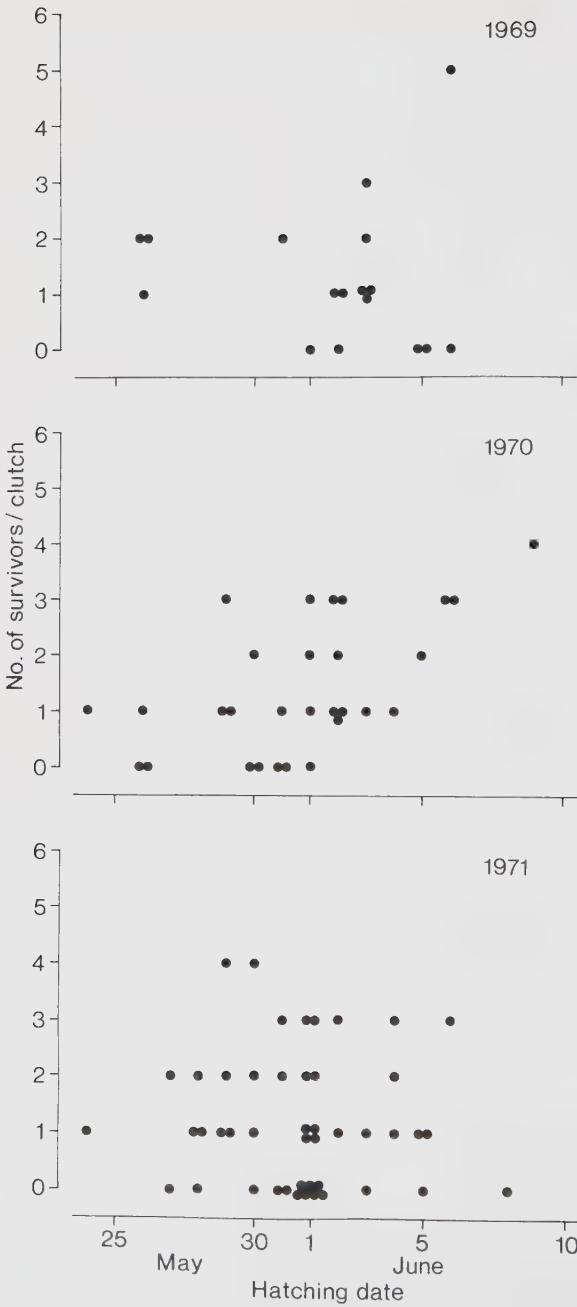
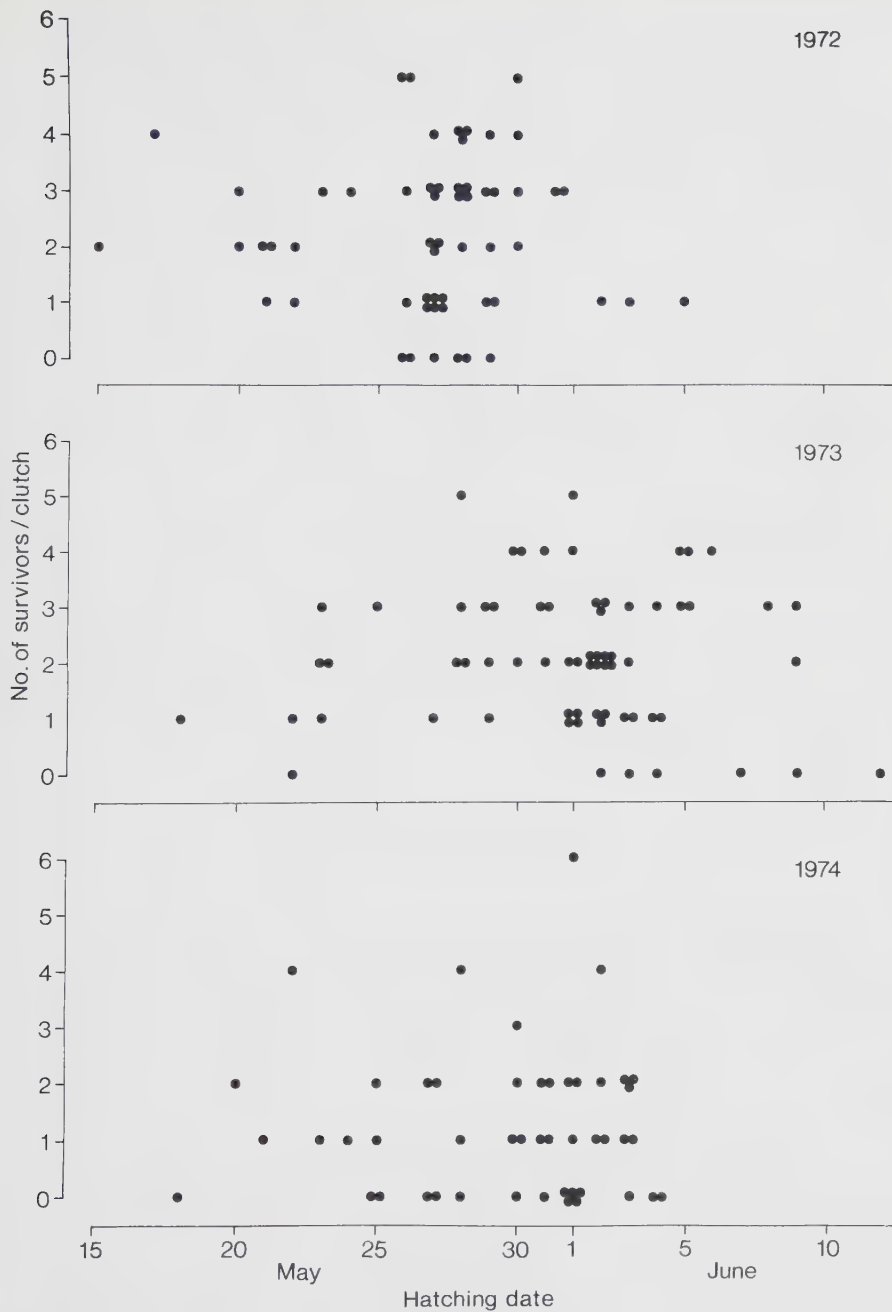


Fig. 7. The number of young fledging per brood in the Great Tit in Linnebjerg in relation to hatching date, 1969-1974.

Fig. 8. Number of young Great Tits from each brood in Linnebjer in 1969-74 known to have been alive at least 3 months after fledging.





χ^2); in these years somewhat more young from early and somewhat fewer young from late broods were controlled. In the other years no statistically significant differences were found, but there was a tendency for the very latest young in all years to produce fewer controls than expected.

The survival of first brood young, plotted against hatching date, is shown for the years 1969 to 1974 in Fig. 8. The low numbers early in 1970 and 1973 reflect poor nestling survival (cf. Fig. 7). The important information of the figure, however, is that, in most years, about equal numbers of young survived from all broods hatching over a period of 2-3 weeks. This differs from the results of Perrins (1965) who found survival rate to be highest for the earliest broods and to decrease, sometimes strongly, with date.

7.1.2 Blue Tit

In the Blue Tit, young were grouped in three classes each year: early, middle, and late fledgers, and the number of controls in each class combined for all years and compared with the expected values; there was a close agreement between expected and observed numbers, but, as pointed out above, there were few late young (almost no second broods).

7.2 In relation to nestling weight

7.2.1 Great Tit

The influence of its nestling weight on a bird's chances of being controlled later was studied (i) by comparing the mean nestling weight of young subsequently controlled with that of all other nestlings, (ii) by comparing the number of young recovered belonging to each of a number of weight classes with that expected, and (iii) by comparing the mean weight of broods that yielded recoveries with that of broods that did not. None of these tests gave statistically significant differences. As a matter of fact, even a few very light young (14.2 to 15.4 g) ringed in 1969 survived and were later found breeding.

Provided the birds that were later controlled constitute a reasonably unbiased sample, the analysis showed, however, that males were on average 0.5 g heavier than females already at the nestling stage ($p < 0.001$; t-test).

7.2.2 Blue Tit

In the Blue Tit, 22 % of the nestlings with weights above the mean of their brood were later controlled against 13 % of those with weights below the mean, this difference being statistically significant ($p < 0.05$; χ^2). This was not an effect of more males (which are heavier than females) being controlled; the difference was present also within the sex categories.

7.3 In relation to brood size

7.3.1 Great Tit

Although larger clutches produced more fledglings than smaller clutches, differential postfledging mortality may nevertheless decrease these differences and make the fitness of birds laying large and small clutches, respectively, more equal. The proportion of young from different brood sizes (at fledging) that survived three months or more was calculated for each year (Tab. 13) and compared with that expected on the assumption of equal survival rates. In none of the years 1969 to 1974, for which data are available, did survival rate differ significantly between brood sizes (χ^2); the agreement between observed and expected values was usually very close and the few discrepancies that were found went in opposite directions in different years. Thus, while the proportion of young surviving from the very largest broods tended to be slightly smaller than expected in 1973 and 1974, the reverse was true in 1971 and 1972. Second broods were too few to allow a proper analysis; combined over the years, 8.4 % of their fledglings were later controlled (10 out of 119), 4 from broods of 1-5 young (7 %) and 6 from broods of 6-9 young (10 %). In summary then, it seems that, once fledged, the young of different sized broods survived equally well.

7.3.2 Blue Tit

Data are too limited to allow much statistical testing, but as in the Great Tit, there was no tendency for survival rate to be related to brood size at fledging, at least within the range observed (6 to 14 young fledging). As the proportion of young later controlled was very similar in 1972 and 1973 (12.5 and 11 %, respectively) it may be reasonable to combine these two years; expected and observed values agreed very closely ($p > 0.5$, χ^2).

Tab. 13. Postfledging survival (> 3 months) of young Great Tits *Parus major* from broods of different sizes. For each year is given the number of young fledging from each brood size and (in italics) the numbers subsequently controlled.

Year	Brood size at fledging													Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	
1969	-	6	-	8	10	-	14	32	36	-	-	12	-	118
	-	2	-	1	3	-	2	4	2	-	-	5	-	19
1970	1	2	9	4	10	24	42	8	45	40	11	-	-	196
	1	0	2	0	1	4	13	2	12	5	3	-	-	43
1971	-	-	-	-	5	-	42	64	54	160	55	36	13	429
	-	-	-	-	0	-	5	7	7	24	3	8	3	57
1972	-	2	-	-	-	12	35	128	108	150	66	12	-	513
	-	0	-	-	-	4	12	25	27	33	20	5	-	126
1973	-	-	-	16	15	36	84	80	144	110	44	12	-	541
	-	-	-	5	4	12	30	16	36	31	5	1	-	140
1974	-	4	3	12	15	18	28	56	117	90	33	-	-	376
	-	0	2	2	2	2	9	12	17	11	4	-	-	61

8. DISCUSSION

8.1 The timing of breeding

8.1.1 First clutches

There are two contrasting views as to what determines the onset of egg laying in the Great Tit (and the Blue Tit). One claims that the timing of laying is adjusted in relation to stressful periods that occur later in the breeding cycle (Lack 1954, 1955, van Balen 1973, Yom-Tov & Hilborn 1981), while the other argues that the females start laying as early as food conditions permit them to do so (Perrins 1963, 1965, 1970, 1973, Lack 1966).

The idea that egg laying is adjusted in such a way that the young are in the nest during the period of highest food abundance was first put forward by Lack (1954) and was based on the work of J.A. Gibb, who found a close agreement between the number of active broods and the amount of caterpillars in the wood (as estimated from frass fall). Lack argued that the proximate control of laying was exerted by photoperiod modified by temperature. The tacit assumption behind this view is that the period when nestlings are being fed is the most demanding time of the breeding cycle. However, van Balen (1973) found that the Great Tits' hatching in oak woods usually took place a few days too late to coincide with the peak abundance of caterpillars. More important, he also found that the nestling period was generally not the most stressful period for the adults as judged from adult weights. Thus, females experienced a higher daily weight loss during incubation and the early part of the nestling stage (when they brood the young for most of the time) than during later nestling stages when the food demands of the brood were largest. He therefore claimed that incubation and the early nestling period together constituted the most difficult period for the parents. On the basis of unpublished observations on fledgling survival and weight loss he also suggested that the post-fledging period might be another difficult time. Peak caterpillar abundance usually occurred between these two critical periods and coincided roughly, but not perfectly, with the period of most rapid nestling growth.

In pine woods, egg laying started at the same time as in oak woods even though the curve of caterpillar abundance was radically different; most often peak abundance was reached much later, sometimes well after the most critical period for first brood young. Because first clutches were started at the same time in the two

habitats, van Balen concluded that the same proximate factors controlled the start of laying; since feeding conditions during spring were thought to be much better in oak woods (higher caterpillar abundance in late April and early May) than in pine woods, food availability could not be involved.

Recently Yom-Tov & Hilborn (1981) performed a simulation based on data from the long-term study of tits at Oxford. According to their simulation, female Great Tits attain enough body reserves for laying eggs about 12 d earlier than laying actually takes place at Oxford. They argued, in line with van Balen (1973), that laying is adjusted to the most critical period for the parents, which coincides with the hatching of the young.

In some other bird species it has similarly been suggested that the females defer laying until the food supply is stable enough to safely carry them over the incubation period, e.g., House Martin Delichon urbica (Bryant 1975), Manx Shearwater Puffinus puffinus (Brooke 1978), Swallow Hirundo rustica (Turner 1981).

In contrast, Perrins (1963, 1965, 1970, 1973) following Toller (1922) argued that the start of laying is determined by the food available to the laying female. Although peak caterpillar abundance often coincided with the time that most pairs of tits had young in the nest, this correlation was both accidental and far from perfect (c.f. data in van Balen (1973)). As young from early broods survived better than young from later broods, females would have produced more surviving offspring had they laid earlier. The reasons they did not, Perrins suggested, was that they were unable to collect enough food and store necessary reserves for the formation of eggs. The evidence in support of this hypothesis will be briefly reviewed here.

(i) Correlation between female weight and time of laying. The observation of Jones (1973) that smaller Great Tit females started egg laying earlier than larger females supports the idea of food limitation; smaller females require less energy for maintenance and should therefore be able to acquire necessary nutrient stores earlier. This argument has been extended in an interspecific comparison. Thus, Dunn (1976) showed that four species of tits at Oxford started laying in order of weight. This, however, could also be explained by the smaller species bringing smaller (i.e. earlier instar) caterpillars to their young. At Lund, Marsh Tits

Parus palustris began to lay on average a week earlier than Blue Tits in the same woods despite the two species being of almost identical weight (Källander 1976); at present the reason for this difference is not known.

It should be noted that a correlation between female weight (size) and laying date was not found by Ojanen et al. (1979), by van Noordwijk et al. (in prep., quoted in van Noordwijk et al. 1981), or in the present study. Jones' (1973) results should therefore be treated with caution.

(ii) Influence of nest-box temperature. O'Connor (1978) and Dhondt & Eyckerman (1979) found that egg-laying in the Great Tit started earlier in better insulated and in warmer boxes, respectively. These results probably mean that females roosting in these at night lost less energy than females roosting in less favourable boxes and were thus able to get into breeding condition earlier. Similarly, Will (1969, quoted in Murphy 1978) found that House Sparrows Passer domesticus started reproducing earlier if their nest was situated inside a building rather than outside, and Murphy (1978) suggested that the reason sparrows laid earlier at one of the farms he studied was that this farm had more heated outbuildings than the other farms.

(iii) Influence of ambient temperature on egg weight and the occurrence of laying irregularities. Jones (1973), in the Great Tit, found a close correlation between deviations in egg weight from the clutch mean and ambient temperature 4 d earlier, and a similar result was obtained for the last egg of the clutch by Ojanen et al. (1981); these authors also studied other species and gave further references to this phenomenon. Perrins (1970) and Jones (1973) also found a positive correlation between egg weight and laying date, which was not simply due to the general trend of rising temperatures in the course of the season, and suggested that the laying of small eggs in the beginning of the season was an adaptation to allow an early start. The relationship between the weights of eggs and the temperatures during their formation might suggest that females are close to an energetic ceiling during the laying phase, but one would perhaps have expected an influence of temperature at a somewhat later stage of egg formation than found by Jones (1973) and Ojanen et al. (1981).

Further support for food limitation comes from the fact that gaps in the laying sequence tend to occur about 2 d after the bird has experienced low ambient temperatures (see Winkel (1970) for Great and Blue Tit, and for references to other species). Low temperatures increase the energy requirements of the female and possibly also influence the availability of insect food, but, for tits, the latter suggestion remains untested. In hunters of aerial insects, suspended laying has been shown to be associated with low insect abundance (House Martin: Bryant 1975, Swift Apus apus: Lack 1956, O'Connor 1979). There was also some indication that females that laid irregularly lost more weight than those that had a regular laying (Bryant 1979).

(iv) Influence of food availability on egg weight. Egg weight correlated negatively with nest density and positively with lumbricid biomass at the most frequented feeding sites between colonies of the Fieldfare Turdus pilaris (Otto 1979). Higher egg weights were also reported in Magpies Pica pica and Starlings Sturnus vulgaris given supplemental food before and during laying (Högstedt 1981, Källander & Karlsson in manuscript).

The relevance of variations in egg weight with food abundance for the question of what determines the onset of laying is difficult to evaluate. One interpretation is that the female lays as soon as she can gather enough food to form an egg above a certain critical size (Jones 1973) and uses any extra energy to increase the size of the egg.

(v) Correlation between food hoarding and start of laying. The early breeding found in nutcrackers Nucifraga spp. has been connected with their reliance on seed stores cached in the preceding autumn (e.g., Turcek and Kelso 1968). But it is not sufficient to establish a correlation between food storage and early breeding; as a matter of fact, the European Jay Garrulus glandarius stores large amounts of acorns in autumn (Bossemma 1979) yet breeds relatively late. One must show that variations in the onset of breeding parallel variations in the amount of food stored. Such evidence comes from studies of the Piñon jay Gymnorhinus cyanocephalus, where Balda and Bateman (1972) found that the time of breeding correlated with the size of the cone crop of the previous autumn (pine seeds being cached in proportion to availability). Similar observations were made by Ligon (1978) who also

recorded breeding in late autumn in years with bumper crops of Pinus edulis seeds. Balda and Bateman (1972) concluded that the seeds stored provide the necessary food for attaining the positive energy balance required for initiating breeding.

(vi) Extra-seasonal breeding. Breeding and breeding attempts outside the normal breeding time have been recorded in several passerines, one of the best studied cases possibly being that of the Tricolored Blackbird Aegelaius tricolor (Payne 1969). In this species, autumnal (extra-seasonal) breeding in a semiarid area correlated either with rain, a local concentration of grasshoppers, or the ripening of irrigated rice. In a laboratory experiment, ovaries remained inactive on a pure rice diet, while growth was stimulated by a rich supply of grasshoppers.

(vii) Length of the pre-laying period. In the migratory Lapwing Vanellus vanellus, which arrives at the breeding grounds in South Sweden in late February or March, Högstedt (1974) found a negative correlation between the amount of earthworms on the territories and the length of the period the females spent there before starting laying.

(viii) Correlation between caterpillar abundance and time of laying. Perrins (1979, Fig. 63) presented data on the abundance of caterpillars of the winter moth Operophtera brumata in Marley Wood, Oxford, over a period of years. I used these data together with those on laying dates (Lack 1966, Tab. 2) to calculate the correlation between caterpillar abundance and the mean date of the first egg of the Great Tits in the same wood and years; the correlation was weak and not statistically significant, apparently because of the strong dependence of laying on spring temperatures. When, however, spring temperatures (warmth sums) were kept constant in a partial regression a negative correlation was obtained. It became weaker, however, when the number of caterpillars per pair was used rather than absolute numbers. These results might mean that the availability of newly hatched caterpillars influences the start of egg-laying; the mean date for the first egg at Oxford usually falls at the time when half the Operophtera caterpillars have hatched (cf. Perrins 1973, Fig. 2 and Lack 1966, Tab. 2). The caterpillars are very small at hatching and may not be important as food for the tits until after a

period of growth. A more careful analysis of the relationship between the caterpillar food supply and the laying dates of the tits should therefore take caterpillar developmental stage (biomass) into account.

(ix) Experimental advancement of laying by the provision of food. My own observations (Källander 1974) that provision of mealworms advanced laying by approximately 5 d refer to the Great Tit (but Blue Tits may also have been affected; see Section 2.3.2 in this paper), and similar results have been obtained in a variety of species: Carrion Crow Corvus c. corone (Yom-Tov 1974); Willow and Crested Tit Parus montanus and cristatus (von Brömssen & Jansson 1980); Song Sparrow Melospiza melodia (Smith et al. 1980); Herring Gull Larus argentatus (Spaans in Drent and Daan 1980); Kestrel Falco tinnunculus (Dijkstra et al. 1982); Red-winged Blackbird Agelaius phoeniceus (Ewald & Rohwer 1982); Starling (Källander & Karlsson in manuscript); and, perhaps, Magpie (Högestedt 1981) and Sparrowhawk Accipiter nisus (Newton & Marquiss 1981).

The strongest evidence in favour of the food limitation hypothesis is the fact that food supplementation results in an advancement of egg-laying, but most, perhaps all, of the observations listed above might be taken to indicate that food or energy is somehow involved in the timing of laying. None, however, is sufficient to show that this timing is brought about by the female's monitoring her body reserves and intake rate as suggested by Jones & Ward (1976) in their important analysis of Quelea reproduction.

At least two serious arguments can be raised against the food limitation hypothesis. First, as noted above, van Balen (1973) found that egg laying by Great Tits started at the same time in deciduous and coniferous woods within the same general area. Caterpillar biomass is probably always much lower in coniferous woods even after taking the lower density of tits into account (sometimes less than one percent of that in deciduous woods as calculated from data in van Balen (1973)). In addition, peak abundance occurs much later in the season. So far, however, food levels in the period immediately preceding laying have neither been measured in deciduous nor in coniferous forest.

The second finding that challenges the food limitation hypothesis is the high degree of heritability of laying date found in the Great Tit (van Noordwijk et al. 1981). Although it is easy to

imagine potential advantages of early breeding (see von Brömssen & Jansson (1980) for a discussion), van Noordwijk et al. (1981) found no selection for early breeding in the long series of Dutch Great Tit data they analysed. On the contrary, in many years, clutches started in the middle or late period produced more recruits to next year's population than the earliest clutches. Also Fig. 8 in this paper shows no seasonal trend in survival rate of first brood young.

Another piece of evidence against the presumed advantages of early breeding in the Great Tit is the fact that the earliest females to lay tend to have a gap of 1-2 days between the completion of the clutch and the start of incubation, while incubation starts progressively earlier in relation to clutch completion as the season proceeds (Zink 1959, Winkel 1970, Neub 1979). This might indicate either an adjustment of hatching date to feeding conditions for the young or more strain on those females that start egg-laying early. In this connection it is worth noting that I found no difference in survival of females starting early and of females starting late, better survival of those starting early otherwise being a possible selective advantage.

To sum up, despite much work, most of which correlational but also some experimental, the proximal factors that govern the start of egg laying remain ill understood. The main difficulty lies in understanding the advancement of laying brought about by food supplementation and its relation to ultimate factors.

8.1.2 Second clutches

Kluyver et al. (1977) analysed the interval between the fledging of the first brood and the laying of the first egg in second clutches of Great Tits in different Dutch study areas. This interval was found to be related to the food situation at the time when first brood young were being raised, being shorter in years of high caterpillar abundance. More important, there was a positive correlation between the length of the interval and the number of young the parents raised from the first brood, suggesting a link with female condition. This was particularly clear in the data from Vlieland, where the production from first broods had been experimentally reduced; in this situation environmental variations could be ruled out as an explanation. Very similar results were obtained by Smith & Roff (1980).

The present study also provides some support for the idea that

variations in individual condition play a role. In 1969 and 1970, many broods were (naturally) reduced in the early part of the nestling period. In these years, both male and female weights at the time first brood nestling were being fed correlated negatively with the number of young in the nest. A likely explanation is that the raising of fewer young than the females had set out to raise enabled them to put on fat; those females starting a second clutch both raised fewer young from their first brood and weighed significantly more than those not starting one. Similar results were obtained in an ongoing experimental study of Great Tits (H. Källander, J.-Å. Nilsson & H. Smith in progr.). Females with reduced broods were significantly heavier ($\bar{x}$ = 20.9 g) than both females with enlarged ($\bar{x}$ = 18.0 g) and females with natural broods ($\bar{x}$ = 18.4 g). Furthermore, no female with an enlarged brood laid a second clutch, whereas 43 % of control and 'reduced' females did. There was also a tendency for inter-brood interval to be negatively related to female weight.

Female Great Tits given an artificial food supply during the incubation and nestling periods were also significantly heavier than control females (den Boer-Hazewinkel 1981), but whether this had any effect on inter-brood interval was not reported. The proportion of second clutches seemed to be unaffected, however.

The negative correlation between brood size and parent weight is, however, also consistent with the idea that parents adaptively lose weight to minimize flying costs during provisioning trips (Freed 1981, Norberg 1981); parents with a smaller brood (fewer feeding trips) could then 'afford' to carry more fat. Freed (1981) found no correlation between brood size and female weight loss, and he used this as an argument against the parent stress hypothesis, i.e. parents losing weight as a result of work connected with provisioning trips. Apparently his analysis was based on unmanipulated broods only, and there is a distinct possibility that birds adjust their clutch size to territory quality and/or individual foraging capacity (Perrins & Moss 1975, O'Connor 1978, Högstedt 1980); if so, one would not expect a negative correlation between female weight and brood size unless the brood had been reduced by some sudden event such as partial predation or adverse weather (as opposed to lasting food scarcity which should be expected to affect parent and/or nestling weights). This adjustment of clutch size will be further discussed below (section 8.2.3).

8.2 Clutch size

Clutch size and its evolution have been extensively discussed, not least in tits. Here only three aspects will be considered.

8.2.1 Clutch size in relation to laying date

In a recent simulation, Yom-Tov & Hilborn (1981) showed that, under the assumptions of their model, it would be advantageous for a Great Tit that starts breeding early to lay a large rather than a small clutch. This was because, by laying a few more eggs, a female would encounter the energetically most demanding period a corresponding number of days later, when both ambient temperatures and food levels are higher. This agrees with the finding in most studies of the Great Tit that clutch size is largest at the beginning of the season. In Linnebjerg, however, clutch size was more or less constant over the laying period of first clutches, and van Balen (1973) and Orell & Ojanen (in press) reported smaller sizes for the earliest clutches in one of their respective areas. van Balen tried to explain his observation with reference to population density, the pattern of increasing clutch sizes being observed in the densest population. He argued that territorial behaviour was strongest earliest in the laying period and that this might have influenced the earliest breeders negatively. It is true that also the observation of Orell & Ojanen refers to their densest population, but the mean density they recorded was only about one sixth that of van Balen's population. Therefore, it seems unlikely that the suggested mechanism could be responsible. Neither is it obvious why high levels of territorial behaviour should prevent females that have already laid a number of eggs from continuing laying, particularly as the food level is increasing and territorial activity decreasing. One would rather suspect that the clutch size pattern observed is an adaptation to local conditions, although it is far from clear which selection pressures have created it.

8.2.2 Clutch size in relation to food abundance

Lack et al. (1957) found that the mean clutch size of Great and Blue Tits was related to the amount of food present at the time young were in the nest, a correlation that was later considered accidental (Perrins 1965, Lack 1966). Klomp (1970) concluded that

the females could not have responded to caterpillar abundance, because the caterpillars are not yet available at the time of laying. Similarly, van Balen (1973) observed that, in most years, the majority of the Great Tits started laying before the leaf buds had bursted and caterpillars become available. However, a comparison of Fig. 2 in Perrins (1973) and Tab. 2 in Lack (1966) shows that, in Wytham, half the Operophtera larvae have normally hatched on the mean date for the start of laying by the tits. The abundance of late instar caterpillars is determined primarily by mortality during the first larval period (Varley & Gradwell 1962, quoted in van Balen 1973), and the situation is further complicated by the fact that the length of the larval period is negatively correlated with the hatching date of the larvae (Perrins 1973, Fig. 2). In addition, Great and Blue Tits bring caterpillars of a large number of species to their young, and it seems to be unknown to what extent their populations vary in parallel with that of Operophtera. Without actual measurements of caterpillar abundance at the time the tit clutches are being produced, it is therefore difficult to judge whether the birds can use food as a proximate cue that predicts, with reasonable reliability, food abundance a few weeks later.

There are, however, some observations which indicate that this might be the case. Perrins (1965) analysed the Great Tit data from Marley Wood (Wytham) for a relationship between the abundance of Operophtera caterpillars (measured at the time of pupation) and clutch size of the Great Tit and concluded that no correlation existed. The data are plotted in Fig. 9. Caterpillar abundance was read from Perrins (1979, Fig. 63) and divided by the number of pairs of Great Tits (Lack 1966, Tab. 2) to obtain an index of availability to each pair. The correlation between caterpillar index and mean clutch size is highly significant ($r_s = 0.80$, $p < 0.001$). The correlation improves slightly if one compensates for the (non-significant) influence of laying date. A positive relationship between mean clutch size and food abundance was also reported in the Bay-breasted Warbler Dendroica castanea (MacArthur 1958), the House Martin Delichon urbica (Bryant 1975), the Nutcracker Nucifraga caryocatactes (Swanberg 1981), and the Redpoll Carduelis flammea (Enemar & Nyström 1981). The latter two species raise their young on seeds, the Nutcracker depending on hazel nuts stored the previous autumn, the Redpoll on birch seeds. In both these cases, the future abundance of food

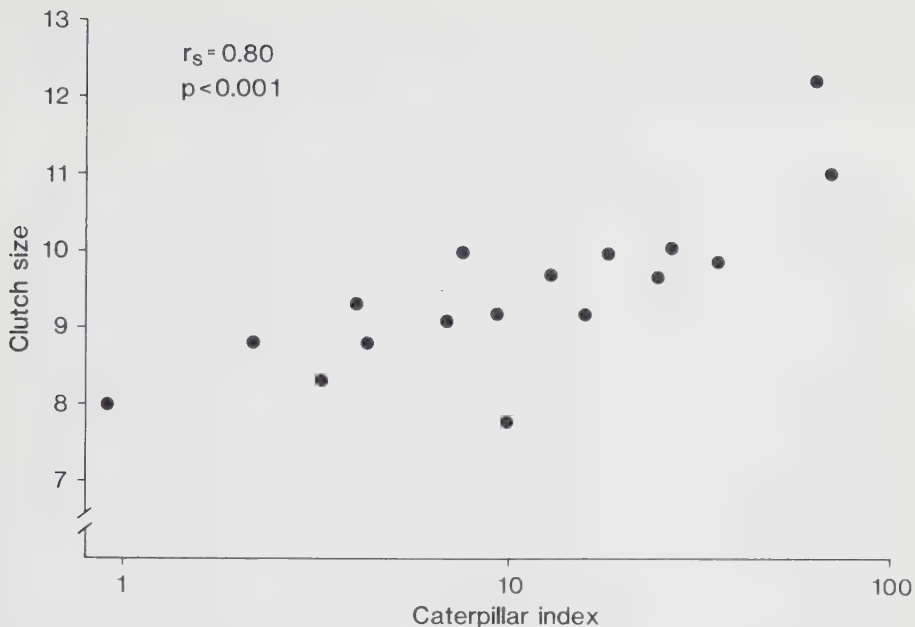


Fig. 9. Correlation between caterpillar abundance and clutch size in Marley Wood, Oxford. The caterpillar index is the number of *Operophtera* caterpillars m^{-2} divided by the number of pairs of Great Tits. Data on caterpillar abundance from Perrins (1979), on clutch size and number of pairs of Great Tits from Lack (1966).

for the young can probably be accurately predicted. The positive relationship in the insectivorous species is more interesting.

In this connection, however, it is appropriate to point out the intriguing fact that, with one possible exception, experimental provision of food during the pre-laying and laying periods has not led to larger clutches in the passerines so far studied (Källander & Karsson in manuscript). This suggests either (i) that these birds do not adjust their clutch size on the basis of food abundance at the time of laying or (ii) that they fail to do so due to the design of the experiments. The number of second clutches did not increase as a result of food being supplied in the nestbox during the first breeding attempt (den Boer-Hazewinkel 1981). This may be regarded as equivalent to the lack of effects on clutch size in other similar provisioning experiments. It may be that the birds do not base their decision on clutch size (or whether or not to lay a second clutch) on the presence of one or a few localized food sources but sample larger portions

of the habitat. This, of course, would be a safer strategy if local food concentrations were ephemeral.

8.2.3 Individual adjustment of clutch size

O'Connor (1978a) placed Great and Blue Tits (with regard to their first, but not to their second clutches) in a group of birds characterized by clutch size adjustment. In these birds food levels were considered to be reasonably stable over the nestling period and, which is important, predictable at the time of laying. The good nestling survival and the fact that the nestlings are normally well nourished are consistent with this view (but this does not apply to all habitats; van Balen (1973), Perrins (1979), Orell & Ojanen (in press)). O'Connor's classification refers to population phenomena, but might, at least partly, be extended to the individual level.

Post-fledging survival did not differ systematically for broods of different size at fledging (Tab. 13), and the largest clutches also produced most fledglings. Furthermore, an analysis of recruitment to the local breeding population (Tab. 14) gave no indication that clutches of different size contributed different proportions of recruits to later generations. Thus, clearly a female Great Tit would increase her short-term fitness

Tab. 14. The number and proportion of Great Tits Parus major hatching from clutches of different size that were subsequently recruited to the local breeding population (1970 includes birds in the adjacent wood Frueråften).

	Clutch size								
	5	6	7	8	9	10	11	12	13
1970: Nos recruited	1	0	4	10	9	24	4	-	-
% recruited	20	0	9.5	15.6	12.5	15.0	12.1	-	-
No. of clutches	1	3	6	8	8	16	3	-	-
1971: Nos recruited	-	-	0	4	2	16	12	7	6
% recruited	-	-	0	12.5	4.4	14.5	6.8	11.7	15.4
No. of clutches	-	-	1	4	5	11	16	5	3
1972: Nos recruited	-	-	1	10	12	13	16	1	1
% recruited	-	-	7.2	13.9	14.8	6.2	12.1	8.3	7.7
No. of clutches	-	-	2	9	9	21	12	1	1
1973: Nos recruited	2	3	4	8	10	9	1	1	-
% recruited	40	12.5	8.2	9.1	7.9	5.3	1.0	8.3	-
No. of clutches	1	4	7	11	14	17	9	1	-

Tab. 15. Mean (S.D.) number of fledglings produced in each year 1969 to 1974 by female Great Tits *Parus major* that survived and disappeared, respectively, to the following breeding season. t-value (Student's t) and its associated p-value also given.

	Survived	Disappeared	t	p
1969	8.40 (3.56)	9.12 (2.85)	0.72	0.65
1970	9.55 (1.86)	8.38 (2.89)	1.18	0.24
1971	9.50 (1.60)	9.21 (1.74)	0.29	0.56
1972	8.82 (1.78)	8.92 (1.44)	0.10	0.82
1973	7.95 (1.86)	8.35 (1.94)	0.40	0.41
1974	7.89 (2.81)	7.22 (2.73)	0.67	0.40

by producing a large clutch. However, adult survival may be negatively related to fecundity, the highest long-term fitness resulting from laying a clutch smaller than maximum (Williams 1966, Stearns 1976). It is therefore interesting to ask whether female survival was influenced by differences in fecundity. As seen from Tab. 15, females that disappeared (i.e. probably died) from one breeding season to the next did not produce more fledglings than did females that survived. Nor was there any difference between the proportion of females that survived and that which disappeared after having fledged more and fewer young, respectively, than the year's median. The same was found for the Blue Tit. These results differ from those for Willow Tit presented by Askenmo & Ekman (in manuscript); in the latter species females that disappeared had significantly more large-grown nestlings.

As discussed by Smith (1981) similar contradictory results with regard to the relation between fecundity and survival have been found in other studies. In the Song Sparrows he studied, there seemed to be a positive relationship between fecundity and female survival, and he suggested that this could be explained by quality differences among individuals (also cf. Högstedt 1981). With regard to clutch size in the Great Tit I would favour this explanation, i.e. clutch size being phenotypically modified to female capacity and to territory quality. If this adjustment is reasonably precise, one would not expect to find any relationship between fecundity and adult survival, nor between adult weight and number of nestlings the parents are feeding (except after a sudden reduction in number of nestlings, e.g., through partial predation; see sections 4.3 and 8.1.2). Also van Balen (1973) concluded that the nestling period is not a critical period for

the parents. Normally, brood size should not influence mean nestling weight either (section 4.1; but cf. Perrins 1965). However, the large clutch size and the high incidence of undernourishment in broods in coniferous forest (van Balen 1973) contradicts the view of a close phenotypic adjustment of clutch size in the Great Tit. It would certainly be most interesting to study the relationship between reproductive effort and adult survival of Great Tits in that habitat.

8. REFERENCES

- Askenmo, C.E.H. & Ekman, J.B. (in manuscript). Reproductive effort in the Willow Tit - is there a dynamic strategy?
- Balda, R.P. & Bateman, G.C. 1972. The breeding biology of the Piñon Jay. Living Bird 11: 5-42.
- van Balen, J.H. 1973. A comparative study of the breeding ecology of the Great Tit Parus major in different habitats. Ardea 61: 1-93.
- Belman, P.J. 1980. Populations of Blue and Great Tits at Perivale Wood. Lond. Naturalist 59: 52-59.
- den Boer-Hazewinkel, J. 1981. Effect of the addition of food during the breeding season on the production of second broods by the Great Tit, Parus major. Verh. Koninklijke Akad. Wetenschappen, Afd. Natuurkunde, Tweede Reeks 77, Institute for Ecological Research, Progress Report 1980: 6-10.
- Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117.
- von Brömssen, A. & Jansson, C. 1980. Effects of food addition to Willow Tit Parus montanus and Crested Tit P. cristatus at the time of breeding. Ornis Scand. 11: 173-178.
- Brooke, M. de 1978. Some factors affecting the laying date, incubation and breeding success of the Manx shearwater, Puffinus puffinus. J. Anim. Ecol. 47: 477-496.
- Bryant, D.M. 1975. Breeding biology of House Martins, Delichon urbica, in relation to aerial insect abundance. Ibis 117: 180-215.
- Bryant, D.M. 1979. Reproductive costs in the House Martin (Delichon urbica). J. Anim. Ecol. 48: 655-675.
- Campbell, B. 1968. The Dean nestbox study 1942-1964. Forestry 41: 26-46.
- Dhondt, A.A. & Eyckerman, R. 1979. Temperature and date of laying by tits Parus spp. Ibis 121: 329-331.
- Dijkstra, C., Vuursteen, L., Daan, S. & Masman, D. 1982. Clutch size and laying date in the Kestrel Falco tinnunculus: effect of supplementary food. Ibis 124: 210-213.
- Drent, R.H. & Daan, S. 1980. The prudent parent: energetic adjustments in breeding. Ardea 68: 225-252.
- Ewald, P.W. & Rohwer, S. 1982. Effects of supplemental feeding on timing of breeding, clutch size and polygyny in Red-winged Blackbirds Agelaius phoeniceus. J. Anim. Ecol. 51: 429-450.
- Enemar, A. & Nyström, B. 1981. (Population fluctuations, food and breeding of the Redpoll Carduelis flammea in a mountain birch forest, Swedish Lapland). Vår Fågelv. 40: 409-426. (In Swedish with summary in English.)

- Frederiksen, K.S., Jensen, M., Larsen, E.H. & Larsen, V.H. 1972. (Some data illustrating time of breeding and number of eggs in tits (Paridae).) Dansk Ornithol. for. Tidsskr. 66: 73-85 (In Danish with summary in English.)
- Freed, L.A. 1981. Loss of mass in breeding wrens: stress or adaptation? Ecology 62: 1179-1186.
- Harvey, P.H., Greenwood, P.J. & Perrins, C.M. 1979. Breeding area fidelity of Great Tits (Parus major). J. Anim. Ecol. 48: 305-313.
- Högstedt, G. 1974. Length of the pre-laying period in the Lapwing Vanellus vanellus L., in relation to its food resources. Ornis Scand. 5: 1-4.
- Högstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210: 1148-1150.
- Högstedt, G. 1981. Effect of additional food on reproductive success in the Magpie (Pica pica). J. Anim. Ecol. 50: 219-229.
- Jones, P.J. 1973. Some aspects of the feeding ecology of the Great Tit Parus major L. Dr. Phil. thesis, Univ. of Oxford.
- Jones, P.J. & Ward, P. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea Quelea quelea. Ibis 118: 547-574.
- Källander, H. 1974. Advancement of laying of Great Tits by the provision of food. Ibis 116: 365-367.
- Källander, H. 1976. (Data on the breeding biology of the Blue Tit Parus caeruleus and the Marsh Tit P. palustris in southwest Scania.). Vår Fågelv. 35: 1-7. (In Swedish with summary in English.)
- Källander, H. 1980. (Great Tit, Parus major, raised in a brood of Blue Tits, P. caeruleus, recaptured eight months after fledging.) Vår Fågelv. 39: 43-44. (In Swedish with summary in English.)
- Källander, H. (in manuscript). The breeding biology of the Great Tit Parus major in some woods in SW Skåne, Sweden.
- Källander, H. & Karlsson, J. (in manuscript). Laying date and breeding performance in the Starling Sturnus vulgaris: effects of supplemental food.
- Klomp, H. 1970. The determination of clutch-size in birds. A review. Ardea 58: 1-124.
- Kluijver, H.N. 1951. The population ecology of the Great Tit, Parus m. major L. Ardea 39: 1-135.
- Kluijver, H.N. 1952. Notes on body weight and time of breeding in the Great Tit, Parus m. major. Ardea 40: 123-141.
- Kluijver, H.N., van Balen, J.H. & Cavé, A.J. 1977. The occurrence of time-saving mechanisms in the breeding biology of the Great Tit, Parus major. In: Stonehouse, B. & Perrins, C.: Evolutionary Ecology: 153-169. London & Basingstoke: MacMillan Press Ltd.
- Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford: Clarendon Press.
- Lack, D. 1955. British tits (Parus spp.) in nesting boxes. Ardea 43: 50-84.
- Lack, D. 1956. Swifts in a tower. London: Methuen.
- Lack, D. 1958. A quantitative breeding study of British tits. Ardea 46: 91-124.
- Lack, D. 1966. Population Studies of Birds. Oxford: Clarendon Press.
- Lack, D., Gibb, J. & Owen, D.F. 1957. Survival in relation to brood-size in tits. Proc. Zool. Soc. Lond. 128: 313-326.

- Ligon, D.J. 1978. Reproductive interdependence of piñon jays and piñon pines. Ecol. Monogr. 48: 111-126.
- MacArthur, R.H. 1958. Population ecology of some warblers of Northeastern coniferous forests. Ecology 39: 599-619.
- Murphy, E.C. 1978. Breeding ecology of House Sparrows: spatial variation. Condor 80: 180-193.
- Neub, M. 1979. Brutbiologische Konsequenzen des asynchronen Schlüpfens bei Kohlmeise (Parus major) und Blaumeise (Parus caeruleus). J. Orn. 120: 196-214.
- Newton, I. & Marquiss, M. 1981. Effect of additional food on laying dates and clutch sizes of Sparrowhawks. Ornis Scand. 12: 224-229.
- van Noordwijk, A.J., van Balen, J.H. & Scharloo, W. 1981. Genetic variation in the timing of reproduction in the Great Tit. Oecologia 49: 158-166.
- Norberg, R.Å. 1981. Temporary weight decrease in breeding birds may result in more fledged young. Amer. Nat. 118: 838-850.
- O'Connor, R.J. 1978. Nest-box insulation and the timing of laying in the Wytham Woods population of Great Tits Parus major. Ibis 120: 534-537.
- O'Connor, R.J. 1978a. Growth strategies in nestling passerines. Living Bird 16: 209-238.
- O'Connor, R.J. 1979. Egg weights and brood reduction in the European Swift (Apus apus). Condor 81: 133-145.
- Ojanen, M., Orell, M. & Väisänen, R.A. 1979. Role of heredity in egg size variation in the Great Tit Parus major and the Pied Flycatcher Ficedula hypoleuca. Ornis Scand. 10: 22-28.
- Ojanen, M., Orell, M. & Väisänen, R.A. 1981. Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. Ornis Fennica 58: 93-108.
- Orell, M. & Ojanen, M. (in press). The effect of habitat, date of laying and density on clutch size of the Great Tit Parus major in northern Finland. Holarct. Ecol.
- Otto, C. 1979. Environmental factors affecting egg weight within and between colonies of Fieldfare Turdus pilaris. Ornis Scand. 10: 111-116.
- Owen, D.F. 1954. The winter weights of titmice. Ibis 96: 299-309.
- Payne, R.B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Redwinged Blackbirds. Univ. Calif. Publ. Zool. 90: 1-137.
- Perrins, C.M. 1963. Survival in the Great Tit, Parus major. Proc. Int. Orn. Congr. 13: 717-728.
- Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus major L. J. Anim. Ecol. 34: 601-647.
- Perrins, C.M. 1970. The timing of birds' breeding season. Ibis 112: 242-255.
- Perrins, C.M. 1973. Some effects of temperature on breeding in the Great Tit and Manx Shearwater. J. Reprod. Fert., Suppl. 19: 163-173.
- Perrins, C.M. 1979. British Tits. London: Collins.
- Perrins, C.M. & Moss, D. 1975. Reproductive rates in the Great Tit. J. Anim. Ecol. 44: 695-706.
- Sasvari, L. 1975. Social dynamics in populations of the Great Tit, Blue Tit, and Marsh Tit. Opusc. Zool. Budapest 15: 129-152.
- Slagsvold, T. 1976. Annual and geographical variation in the time of breeding of the Great Tit Parus major and the Pied Flycatcher Ficedula hypoleuca in relation to environmental phenology. Ornis Scand. 7: 127-145.

- Smith, J.N.M. 1981. Does high fecundity reduce survival in Song Sparrows? Evolution 35: 1142-1148.
- Smith, J.N.M., Montgomerie, R.D., Taitt, M.J. & Yom-Tov, Y. 1980. A winter feeding experiment on an island Song Sparrow population. Oecologia 47: 164-170.
- Smith, J.N.M. & Roff, D.A. 1980. Temporal spacing of broods, brood size, and parental care in Song Sparrows (Melospiza melodia). Can. J. Zool. 58: 1007-1015.
- Stearns, S.C. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47.
- Swanberg, P.-O. 1981. (Clutch size in the Thick-billed Nutcracker Nucifraga c. caryocatactes in Scandinavia in relation to the supply of hazel nuts in the individual winter stores.) Vår Fågelv. 40: 399-408. (In Swedish with summary in English.)
- Tollenaar, D. 1922. Legperioden en eierproductie bij eenige wilde vogelsoorten, vergeleken met die bij hoenderassen. Meded. Landbouwhoogeschool Wageningen 23 (2): 1-46.
- Turner, F.J. & Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. Commun. Behav. Biol., A 1: 277-297.
- Turner, A.K. 1982. Timing of laying by Swallows (Hirundo rustica) and Sand Martins (Riparia riparia). J. Anim. Ecol. 51: 29-46.
- Vilbaste, H. 1982. (On the nesting time of the Great Tit in the south-western part of Estonia.) Looduskaitse Teaduslikud Tõed 3: 129-137. (In Estonian with summary in English.)
- Williams, G.C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. Amer. Nat. 100: 687-690.
- Winkel, W. 1970. Experimentelle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise (Parus major und P. caeruleus). J. Orn. 111: 154-174.
- Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the Crow (Corvus corone L.). J. Anim. Ecol. 43: 479-498.
- Yom-Tov, Y. & Hilborn, R. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia 48: 234-243.
- Zink, G. 1959. Zeitliche Faktoren im Brutablauf der Kohlmeise (Parus major). Vogelwarte 20: 128-134.

ADVANCEMENT OF LAYING OF GREAT TITS BY THE PROVISION OF FOOD

In his study of the Great Tit *Parus major* in Wytham wood near Oxford, Perrins (1965) observed that young from early broods survived better than those from later broods. He therefore suggested that birds breeding early would be at an advantage and that there would consequently be selection for this character. He thought that 'the tit does not inherit a tendency to breed early or late, but merely a tendency to breed as early as it can'. Since in any year many tits breed later than the optimal date, some factor must exist that prevents them from breeding earlier. Perrins suggested that the most likely factor is the availability of food to the laying female. Later he extended this hypothesis to other species (Perrins 1970). Although much circumstantial evidence exists in support (Immelmann 1971), it seems that the hypothesis has not previously been tested experimentally. In 1972 and 1973, I set up trials to investigate the effect on breeding date of Great Tits provided with additional food.

The experiments were performed in a mature oak-hazel wood, 24 ha in area, situated in agricultural land 10 km northeast of Lund, in which, since 1969 160 nest-boxes had been used by about 50 pairs of Great Tits each year. In 1972, 33 simple roofed feeding

trays were placed in the eastern third of the wood, the rest of the wood acting as a control area. From 11 April onwards each tray was supplied daily with *c.* 20–35 g of mealworms. Previous mapping showed that on average two trays were present in each Great Tit territory. The provision of food continued until 27 April. In order to eliminate variation due to qualitative differences in various parts of the wood, the feeding trays were moved to the western quarter of the wood in 1973. Thirty-two trays were used, on average slightly over 1.5 per territory. The provision of mealworms started on 10 April and continued until 14 May, at a rate of *c.* 35 g per tray daily.

In both years it took one or two days for the tits to start to utilize the mealworms. After a while, however, they learned to associate me with the feeding, and often flew down in advance of me to the (still empty) trays. They then waited on nearby branches while I was filling the trays, and when I moved on would immediately dive down to the mealworms. The trays were normally filled in the mornings and by about noon they would be empty.

Not all the mealworms were taken by Great Tits. Nuthatches *Sitta europaea* were a problem, since they often flew off with a beakful of worms which they hid in bark crevices. Some of these mealworms were subsequently used by Great Tits; on two occasions I observed Great Tits find and eat mealworms that had been stored by Nuthatches. A Nuthatch territory may be equal in area to ten Great Tit territories, and some food was undoubtedly brought into the unfed part of the wood by this means. Chaffinches *Fringilla coelebs* also took mealworms from the trays, and efforts to exclude them were unsuccessful.

The fact that Great Tits to some extent tolerated neighbours at the feeding trays meant that occasionally birds from the unfed part had some access to mealworms. Nevertheless most mealworms were taken by Great Tits resident in the fed areas.

In both years laying was observed on regular inspections of the nest boxes, and the date of the first egg calculated on the assumption that one egg is produced per day. In 1972 the provision of mealworms ceased when only eight Great Tits had started laying, but in 1973 mealworms were available to females until all but four had begun to lay.

TABLE 1

Dates of laying by Great Tits in fed and unfed parts of the wood. Dates are transformed on a scale from day 1 = 20 April. Levels of significance were calculated by the students' t-test¹

		UNFED		FED		Differ- ence (days)	Level of significance (P)
		n	Mean date of 1st egg	n	Mean date of 1st egg		
1972	All females	34	16.4	23	11.7	4.7	< 0.001
	Older females	20	15.5	7	12.4	3.1	> 0.1
	1-year-old females	14	17.6	16	11.8	6.3	< 0.001
1973	All females	41	20.9	21	15.0	5.9	< 0.001
	Older females	16	17.9	12	14.2	3.7	< 0.01
	1-year-old females	25	22.8	9	16.1	6.7	< 0.001

Note: ¹ Since the distributions are not perfectly symmetrical it can be argued whether use of the *t*-test is admissible. Using a non-parametric test (χ^2) does not, however, change the results appreciably: for example, for one-year-old females in 1973 the significance becomes $P < 0.002$.

RESULTS

As shown in Table 1, the mean date of start of laying in the fed part of the wood was invariably earlier than in unfed parts. If one-year-old and older females are treated separately (almost all females were previously ringed) the differences in the start of laying are statistically significant, except among older females in 1972. In 1970 and 1971, when

no provision of food took place, no significant differences occurred between the various parts of the wood.

In the Great Tit, as in several other birds (Perrins 1970: 248), it has been known for long that older females lay earlier than young ones (Kluyver 1951, Perrins 1965, van Balen 1973). Jones (1970) found also that smaller females tended to lay earlier than larger birds. To test for such differences in my material, female weight (which partly reflects size) was plotted against date of first egg. The female weights were obtained when they had young about ten days old, and were taken by night at about the same time o'clock. All regressions are negative, i.e. heavier females tended if anything to start breeding earlier. The correlation coefficients are, however, low, ranging from -0.11 to -0.34 , only one being statistically significant.

The results do not reject Perrins' hypothesis that food sets a limit to the early commencement of laying by Great Tits in spring. It cannot, of course, be ascertained whether it is the amount of food ingested or the amount of food seen that causes earlier breeding. The possibility exists that food acts as a visual stimulus, subsidiary to photoperiod (Suomalainen 1937) and temperature (Kluyver 1952, Perrins 1965, van Balen 1973, and others). This is one of the possible explanations why two pairs of Barn Owls *Tyto alba* kept under conditions of surplus food started to breed unusually early (Bühler 1965).

The artificial provision of mealworms affected one-year-old more than older females. As mentioned above the normally later start of breeding by one-year-old females has tentatively been attributed to their lack of experience (Perrins 1965: 639) and consequently reduced ability to collect the necessary amount of food for forming eggs. This would perhaps explain why they responded more strongly to the artificial provision of food, and would also indicate the importance of nutrition as such. This is also a function of courtship feeding which contributes a substantial proportion of the food to laying female Great Tits and Blue Tits *Parus caeruleus* (Royama 1966, Krebs 1970).

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REFERENCES

- VAN BALEN, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-93.
- BÜHLER, P. 1965. Experimentell ausgelöste Frühbruten bei der Schleiereule (*Tyto alba*). *J. Orn.* 106: 347.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. In: Farner, D. S. & King, J. R. (Eds), *Avian Biology*, Vol. 1. Academic Press. pp. 341-389.
- JONES, P. 1970. Food as a proximate factor regulating the breeding season of the Great Tit (*Parus major*). *Proc. XV Congr. Intern. Ornith.*, p. 657.
- KLUYVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea* 39: 1-135.
- KLUYVER, H. N. 1952. Notes on body weight and time of breeding in the Great Tit, *Parus m. major* L. *Ardea* 40: 123-141.
- KREBS, J. R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. *Ibis* 112: 108-110.
- PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34: 601-647.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255.
- ROYAMA, T. 1966. A re-interpretation of courtship feeding. *Bird Study* 13: 116-129.
- SUOMALAINEN, H. 1937. The effect of temperature on the sexual activity of non-migratory birds, stimulated by artificial lighting. *Ornis Fenn.* 14: 108-112.

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Summer disappearance and postfledging weight loss of Great Tits *Parus major*

Perrins (1965) thought that most juvenile mortality in the Great Tit Parus major occurred in summer during the period immediately after fledging. It has proved difficult to study population phenomena in Great Tits at this time of the year, and consequently few estimates of juvenile mortality exist. Some data for the first two weeks after nest-leaving were given by de Goede (1982), while Dhondt (1979) calculated survival rates until the beginning of September.

In this note I present some additional calculations of juvenile disappearance and on juvenile weight loss during the weeks following nest-leaving. Some observations relating to juvenile dispersal are also reported. The data are based on a study of Great Tits in Linnebjerg, a 24 ha oak wood some 10 km east of Lund, Skåne (for a description see Källander 1976 and in manuscript).

RESULTS

Juvenile disappearance

In 1972, 514 Great Tits were individually colour-ringed as nestlings in Linnebjerg in June. In July and August I tried to identify as many as possible of them in the wood. The cumulative curve of sightings of individuals not recorded earlier levelled off by 1 August at around 182 individuals, i.e. about a third of those initially ringed. Extensive mist-netting in the following winter together with later controls showed that at least 65 of these were still alive by 1 November. Thus 64 % had disappeared in the three months between 1 August and 1 November. Another 65 individuals which had never been recorded in summer were later found alive. Assuming that fraction of the population had been exposed to a similar mortality (disappearance) rate, the total juvenile population by 1 August comprised 361 individuals, i.e. some 30 % had disappeared between fledging and 1 August, a period of about 45 days, giving an average disappearance rate of only $0.67 \% d^{-1}$.

This calculation does not, however, take mortality occurring during the sampling period into account. Since the estimate is sensitive to changes in the number of birds recorded on 1 August, it is perhaps safest not to rely too much upon it. As a matter of fact, calculations based only on sightings in the first and second half of July, respectively, give mean disappearance rates of 1.6 and 1.2 % d^{-1} . Furthermore, no new individuals were recorded in August despite 64 are known, and 179 calculated, to have been alive. The most likely explanation is that most of them had left the wood; winter recaptures were made both in Linnebjerg and in nearby Frueråften. A minimum survival rate of 25 % between fledging and 1 November 1972 is however beyond doubt (i.d. a mean disappearance rate of approx. 0.55 % d^{-1}).

A similar calculation can be made on data from 1973. In that year I mist-netted 93 birds (out of 544 ringed as nestlings) at water in Linnebjerg on average 20 days after their nest-leaving (range 9-32 days). Thirty-six of these were known to be alive on 22 October (38.7 %). Another 103 individuals that were not caught in July were also alive on 22 October. Using the same kind of calculation as above, one arrives at an estimated population of 359 juvenile individuals some three weeks after mean fledging date. This means a disappearance rate of 1.5 % d^{-1} for the immediate post-fledging period. The mean daily disappearance rate between fledging and the end of October was 0.59 % d^{-1} , which indicates that mortality may have been higher in the early post-fledging period than later in the autumn. Weinzierl & Hollenbach (1963) reported a mortality of only 39 % from 1 September to 1 April, but do not give further details.

The minimum survival rate between fledging and early winter was strikingly similar in the two years, about 25 %. This figure should be compared with the 22 % calculated by Dhondt (1979) for the period between fledging and early September.

Post-fledging weight loss

Over the period of 9 to 32 days (mean 20) between nest-leaving and capture, the majority of the 93 fledglings mist-netted in July 1973 had lost weight. The mean nestling weight on their 15th day was 17.98 g (S.D. 1.12), while the corresponding weight in July was 16.92 g (S.D. 0.89), i.e. a highly significant decrease of 1.06 g (5.9 %). Only four of the young had increased in weight,

and another four had the same weight as on their 15th day. There was no correlation between the time they had been out of the nest and the amount of weight loss. Rather surprisingly, however, young that were heavy as nestlings had lost proportionally more than those that were light (Fig. 1). This relation is not easy to understand. One possible explanation could be that light young were slightly younger than their siblings and attained maximum nestling weight a few days later, in which case the correlation would be merely an artefact. Although hatching is not absolutely synchronous (Neub 1979), all young usually hatch within two days, so this explanation does not seem very likely. Furthermore, the heaviest young had weights far above the maximum weight attained by the majority of Great Tit nestlings.

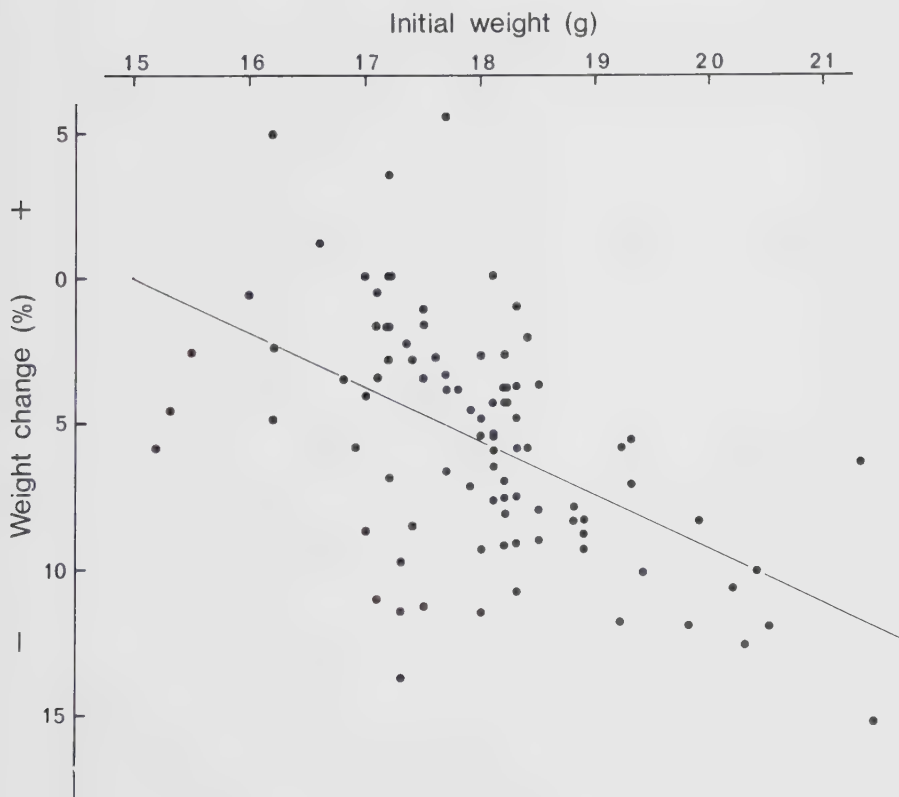


Fig. 1. Relative weight change (%) of juvenile Great Tits during the first period after nest-leaving in relation to nestling weight on the 15th day (initial weight).

Juvenile dispersal

Dispersal may be an important component of juvenile disappearance, particularly if density dependent, and if a nestbox area is surrounded by woods with low tit densities. Especially in the summer and autumn of 1971, attempts were made to quantify dispersal by comparing the proportion of ringed to unringed juveniles at various distances from my nestbox areas. These attempts were not very successful. The main problem with this kind of approach is that the density of tits in the various areas visited is unknown; for that reason the observed proportions of ringed birds cannot be converted to absolute numbers. Yet such observations may contribute to a general picture of juvenile dispersal.

Timing. Juvenile Great Tits seem to start dispersing soon after becoming independent. In 1972, all observations of known individuals within Linnebjerg were plotted on a map. Between day 7 and day 24 after fledging, the distance between the nestbox where a tit had been born and the place of observation increased by 8.5 m d^{-1} ($r = 0.25$, $n = 79$, $p < 0.05$). The registrations indicated a general increase in activity range, but possibly also directed movements take place very soon after independence, i.e. birds moving away and settling in a new area (true dispersal).

In the July sample of 1973, 3 % of the mist-netted juveniles were unringed and therefore almost certainly immigrants. Since the summer population was of a very similar density in 1977, this figure might be compared with the data given by Dhondt (1979). From his Fig. 2 one can calculate that, by 25 July, nearly a fifth of the juveniles in Linnebjerg were immigrants, i.e. some 40 days after mean fledging date. This agrees with my scanty data from 1972, also a high density year. In that year breeding was slightly earlier (Källander in manuscript): on 28 June 3 % of the observed juveniles in Linnebjerg were immigrants, the proportion then rising quickly in the first half of July.

Also observations in other areas indicate a high degree of mobility in July. Some 30 % of the juvenile Great Tits counted in Råften¹⁾, an oak plantation 1.8 km from Linnebjerg, in the second half of July 1971 had been ringed as nestlings in the latter wood. This estimate is based on a total of 131 sightings on five different days, but it is not known to what extent the same individuals were counted on different visits. In 1973, two ringed juveniles, one from Linnebjerg and one from nearby Frueråften,

were seen together with an unringed young Great Tit in a small spruce plantation 3.1 km from the place of ringing some five weeks after nest-leaving.

Dhondt (1979) concluded that there are two main periods of juvenile dispersal, one in July, the other in September, with an intervening period when the birds moult. The fact that only 3 % of the juvenile Great Tits seen 2-3 km from the nestbox areas in August 1971 were ringed, against 8 % in September, gives some support to this conclusion. The total numbers recorded were low, however, only 35 and 143. In agreement with this, no recaptures of Great Tits ringed as nestlings 0.8-4 km from Hammarö bird observatory were made at the observatory before September, whereas several controls were made in June and July of birds ringed as nestlings within 0.5 km (Ehrenroth 1976).

Dispersal distances. Dhondt (1979), who worked with birds that I had previously ringed as nestlings in Linnebjerg, found that 80 % of the male juvenile Great Tits were mist-netted within c. 500 m of their birth place in July, while the same proportion of the females was captured within 900 m. On the basis of this result he concluded that summer movements beyond 2 km were unusual in the Linnebjerg population. Although this conclusion cannot be drawn from the results presented (clearly the numbers of birds captured at different distances from their birth area must be related to the intensity of catching), the statement may still be true.

Among the tits Dhondt captured in Frueråften (1 km) and Råften (1.8 km), 40 % and 17.5 %, respectively, had been born in Linnebjerg, whereas no Linnebjerg-born Great Tit was among the 48 individuals caught at Albacken (2.7 km) (A. Dhondt pers. comm.).

My own captures in winter 1972/73 may also give some idea about dispersal distances, but, it must be admitted, winter movements cannot be ruled out. Of 277 Great Tits captured in Frueråften, about 30 % were juveniles from Linnebjerg. In a beech wood near S.Sandby (4.5 km) this proportion was 3.1 % (6 out of 194), whereas none of 79 at L.Abusa (6.5 km) originated from Linnebjerg.

In spring 1974, 5 out of 27 (18.5 %) Great Tits in Råften had been ringed as nestlings in Linnebjerg, but it could not be established whether all had been born in 1973. At another locality 2.2 km from Linnebjerg none of 27 Great Tits (16 of which territory-holding males) came from Linnebjerg.

¹⁾ called Kungsmarken i Dhondt (1979).

Relation to nestling weight and time of fledging. Although my material on dispersal in relation to weight is very small, it supports Dhondt's (1979) results. Thus I found no relation between weight and dispersal; of 19 birds known to have dispersed longer distances, 14 had nestling weights above the mean for the wood in that year, whereas 5 had weights below the mean. Nor was there any bias with regard to hatching date (for instance, young from late broods showing a stronger tendency to disperse). There was, however, one observation that might be indicative of a 'brood effect'. Two females from the same brood were later controlled in the same direction, 4.5 and 8.2 km from Linnebjer (one in winter and one just before the onset of breeding).

Relation to density. O'Connor (1980) showed a positive correlation between the proportion of long-distance recoveries (> 10 km) and population density as reflected in the British Common Birds Census data. The strength of migration, e.g. at Falsterbo, is likewise density dependent, both in the Great Tit and in the Blue Tit P. caeruleus (Svensson 1981, Källander in manuscript). So far, however, it remains to demonstrate that also the early postfledging (summer) dispersal shows a positive relation with density. As Fig. 2 shows, the rate of immigration may be negatively related to density, a conclusion also drawn by Webber (in Krebs & Perrins 1978).

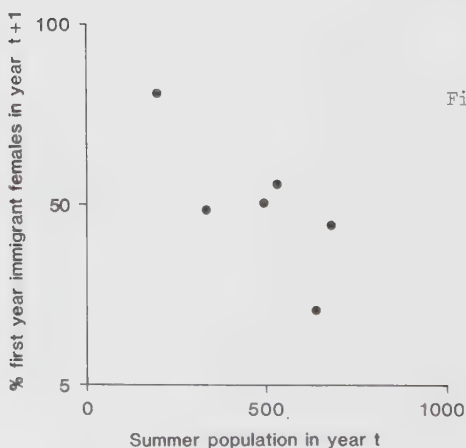


Fig. 2. The proportion of first year females of Great Tits in Linnebjer in relation to the size of the population in the previous summer.

DISCUSSION

The disappearance rates I calculated for the period from fledging until 1 November were very similar in 1972 and 1973, on average 0.55 and 0.59 % d^{-1} , and thus considerably lower than that calculated by Dhondt (1979), i.e. 78 %, or on average 1 % d^{-1} for a period nearly two months shorter. This could reflect a poorer survival in 1977; the population decreased from 60 pairs in 1977 to 31 in 1978. It is also possible that a proportion of the juveniles survived but escaped from being netted, thus influencing the capture-recapture calculations.

Webber (in Krebs & Perrins 1978) monitored the changes in the juvenile:adult ratio from the time the young left the nest until the next breeding season. Assuming adult mortality is constant over the year (which may not be quite true) and about 50 % yearly, one can estimate the disappearance rate of the juveniles at approximately 30 % per month. This agrees with Perrins' (1980) statement that up to 60 % of the young might die prior to August.

Dhondt (1979) found no difference in the disappearance rate between the first five weeks after nest-leaving and the following five weeks, while my calculations indicated that disappearance rate was in fact higher in the first weeks after the young fledged. de Goede (1982) followed three Great Tit broods from fledging until independence and found an overall mortality of 23 % over two weeks, i.e. a mean daily mortality of 1.62 %. But half the mortality fell on one brood and took place on the day of fledging. Thus, mortality over the remaining days was only 13 % or, on average, 1 % d^{-1} . The same author reported disappearance rates of 33 to 43 % for the same period in three other years, calculated from capture-recapture data. No recaptures at all were made from some 15 % of the broods, however. Since at least some of them may have been brought outside the study area by their parents (see observations reported below), de Goede felt it might be justified to omit them from the mortality calculations. The resulting figures for the mortality taking place during the fledglings' dependency period (15-30 %) came much closer to the ones found for the closely followed broods. On present evidence it cannot be safely stated whether the mortality rate is higher during the first weeks after the young have left the nest.

It has been observed that some broods produce no recoveries at all, while several young may be recovered from others (e.g.,

Perrins 1965, own unpublished data). The 93 juvenile Great Tits mist-netted in July 1973 came from 43 different broods out of a total of 68 raised in the wood (63 %). Thus 25 broods were not represented in the sample. From four of these no bird was ever found, while two of the 43 broods that were represented failed to produce later recaptures.

Early postfledging disappearance may have different causes. Apparently parent tits sometimes move away with their still dependent brood. This was recorded at least four times in the present study: in 1969 (1.3 km; B. Cavallin pers. comm.), and in 1971 (0.8, 1.5, and 1.5 km, respectively; own observations). Both immigrant first year parents and older birds were involved.

Predation is another reason why juveniles disappear. In September 1973, rings from 10 Great Tits ringed as nestlings were found in pellets of a Tawny Owl Strix aluco. None of the young was among those mist-netted in early July, and three came from the same brood. Especially the latter observation indicates that they had been taken while still dependent, probably soon after nest-leaving.

A third factor that may cause early losses is starvation. Perrins (1965) observed a positive relationship between nestling weight and recapture rate, a correlation that was further substantiated by D. Moss (see Perrins 1980, Fig. 3). Perrins (1965) thought that mortality from starvation was heavy during the first weeks or month after nest-leaving, affecting young of different weights differentially. Later Garnett (1981) showed that most of the variation in weight was explained by size differences rather than by differences in fat stores, and, in an aviary, he was able to demonstrate a slight positive influence of size (tarsus length) on the outcome of dominance interactions. If large individuals dominate smaller ones, this could have the effect that the latter have difficulties in obtaining enough food and might lose weight and die, or they might disperse. However, dispersing individuals were neither smaller nor had lower nestling weights (Dhondt 1979, present study). Garnett (1981) stated that the fat reserves could not be important for the immediate postfledging survival, since they would at most cover one day's requirements (on average they amounted to 1.08 g, or 7 % of the bird's body weight). This does not mean fat reserves are unimportant, however. Although fairly small they may be important as buffers, supplementing low intake rates when necessary. Since larger birds carried more fat, the

possibility that fat reserves play a role in the differential disappearance of fledglings should not be excluded. Yet, in my study, there was no relationship between nestling weight and subsequent recapture rate in the Great Tit, but there was one in the Blue Tit (Källander in manuscript). In 1973, for instance, Great Tits with a nestling weight above 16.5 g and those weighing 16.5 g or less had identical recapture rates, just below 26 %. It could be that fat reserves are important in some years but not in others. Dhondt (1971) reported a positive correlation between recapture rate and temperature during the breeding season, and Klafs et al. (1981) found a similar correlation with the proportion of juvenile tits in the late summer population. One possible explanation for the larger postfledging decrease in weight of heavy young (Fig. 1) could be that, in fine weather (such as prevailed in late June and early July 1973), there is no advantage in carrying extra fat.

REFERENCES

- Dhondt, A.A. 1971. The regulation of numbers in Belgian populations of Great Tits. Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970): 532-547.
- Dhondt, A.A. 1979. Summer dispersal and survival of juvenile Great Tits in southern Sweden. Oecologia 42: 139-157.
- Ehrenroth, B. 1976 (Movements of tits Paridae at Hammarön Island in northern Lake Vänern.) Vår Fågelv. 35: 261-278. (In Swedish with summary in English.)
- Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, Parus major. Ibis 123: 31-41.
- de Goede, P. 1982. The survival of juvenile Great Tits in the first two weeks after fledging. Verhandl. Ned. Akad. Wetenschappen, Afd. Natuurk. 79, 2. Reeks, Institute for Ecological Research, Progress Report 1981: 7-9.
- Källander, H. (in manuscript). Breeding phenology, clutch size, and fledging success in the Great Tit Parus major and the Blue Tit P. caeruleus in a South Swedish oak wood.
- Källander, H. (in manuscript). Density dependent migration of Great and Blue Tits.
- Klafs, G., Müller, H. & Weber, H. 1981. Zum Einfluss der Witterung während der Brutzeit auf Grossräumige Abundanzänderungen waldbewohnender Singvogelgruppen. Arch. Naturschutz u. Landschaftsforsch., Berlin 21: 227-240.
- Krebs, J. & Perrins, C. 1978. Behaviour and population regulation in the Great Tit (Parus major). In: Ebling, F.J. & Stoddart, D.M. (Eds.) Population control by social behaviour. Institute of Biology, London: 23-47.
- Neub, M. 1979. Brutbiologische Konsequenzen des asynchronen Schlüpfens bei Kohlmeise (Parus major) und Blaumeise (Parus caeruleus). J. Orn. 120: 196-214.
- O'Connor, R.J. 1980. Pattern and process in Great Tit (Parus major) populations in Britain. Ardea 68: 165-183.

- Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus major L. J. Anim. Ecol. 34: 601-647.
- Perrins, C.M. 1980. Survival of Great Tits, Parus major. Acta XVII Congr. Int. Orn. Berlin: 159-174.
- Svensson, S. 1981. (Population fluctuations in tits Parus, Nuthatch Sitta europaea, and Treecreeper Certhia familiaris in South Sweden.) Proc. Second Nordic Congr. Ornithol. 1979: 9-18. (In Swedish with summary in English.)
- Weinzierl, H. & Hollenbach, H. 1963. Untersuchungen über Altersaufbau, Schwankungen u. Wanderungen einer Kohlmeisen und Blaumeisenpopulation des Donau-Auwaldes. Orn. Mitt. 16: 131-136.

Density dependent migration of Great and Blue Tits

The point I want to make in this note is that migratory movements in the Great and Blue Tits Parus major and P. caeruleus are density dependent, i.e. the numbers involved in autumn movements are an increasing function of population density. I also tentatively suggest that the majority of tits recorded at Falsterbo, southwesternmost Sweden, are recruited from South Sweden.

METHODS, DATA

In the following analysis I correlate the numbers of tits ringed in autumn at some bird observatories with data on the size (density) of breeding populations in the preceding summer. It would have been desirable to have an index of late summer populations, but such data are lacking. Clutch size is known to decrease with increasing population density, as is the number of young fledged per pair (e.g., Kluijver 1951, Lack 1966, von Schantz 1981), but both have little influence on the size of the late summer population. Also the frequency of second broods is negatively related to density (Kluijver 1951). Thus, there is some tendency for these factors to make differences between years smaller than those reflected by spring figures. Clearly, spring data also fail to reflect occasional poor breeding success such as that found in Central Sweden in 1981, when first broods of the Great Tit produced on average 1.95 fledged young against a mean of 7.29 (Borgström in press); this no doubt is a serious weakness.

Data on breeding population densities, both published and unpublished were gathered from a large number of localities in Europe (van Balen, Hildén, Källander & Schmidt in prep.); the series were of varying length and involved populations of varying sizes. Here I use some of these data, particularly those from Sweden.

Migratory movements of tits are best reflected by the ringing figures from the bird observatories (most observatories do not carry out counts of visible migration, and, at least at Falsterbo, ringing numbers for the Great and Blue Tits correlate well with numbers counted on migration (Lindskog & Roos 1979)). There are, however, some problems in using data from bird observatories. First, trapping

efficiency may vary from year to year. For instance, difficulties in recruiting staff for the whole autumn period are wide-spread. This was the case even for a well-reputed observatory such as Col de Bretolet in the Swiss Alps (L. Jenni in litt.). Second, at many bird observatories, ringing routines and efficiency have changed, either abruptly due to the introduction of new techniques or more gradually as a result of vegetation changes that have influenced the trappability of the birds. There has also been a clear tendency, perhaps most pronounced at newly established observatories, to increase trapping efforts. This lack of standardization is a serious drawback to any attempt at analysing population fluctuations and population trends from ringing data. Third, many bird observatories have not been in existence for long enough to make comparisons with population data meaningful, or data on the number of birds ringed each autumn are (effectively) unavailable. All these factors together seriously reduced the number of observatories whose data could be used; some details about the material are given in Tab. 1.

Tab. 1. Bird observatories from which ringing data were used.

Bird observatory	Years	No. of years from which useful data exist	Source
Col de Bretolet	1957-81	17	Winkel 1974, L.Jenni in litt.
Col de La Golèze	1966-73	8	Frelin 1975
Mettnau	1972-78	7	Bairlein 1981 (Blue Tit)
Courland Spit	1957-66	10	Odintsova 1975 (Blue Tit)
Courland Spit	1960-76	17	Dolnik & Paevski 1979
Pape	1967-71	5	Lipsbergs & Rute 1975
Ottenby	1957-81	25	Hjort et al. 1981
Falsterbo	1962-81	20	G.Roos in litt.
Hartsö-Enskär	1970-81	12	L.Wahlén pers. comm.

CORRELATIONS BETWEEN THE OBSERVATORIES

Ringing figures for different observatories show a low degree of covariation. In the Great Tit, only three statistically significant correlations were found. As expected, there was a good agreement between the figures from Pape and Courland Spit ($p < 0.01$), both observatories situated on the eastern coast of the Baltic. Also

numbers at Ottenby correlated with those at Courland Spit, but this correlation disappeared completely when the two years 1975 and 1976 were excluded. In these years, large numbers of Russian Great Tits were wind-driven across the Baltic, and the numbers ringed at Ottenby by far exceeded those of earlier years (Lindholm 1978). The third correlation was between Falsterbo and Col de La Golèze ($p < 0.01$) and may have been purely accidental.

The situation was similar in the Blue Tit data. There was a good agreement between Pape and Courland Spit ($p < 0.02$). Ringing totals at Ottenby correlated with the indices given by Odintsova (1975) from Courland Spit, but not with the longer series of ringing figures from the same locality (Dolnik & Paevski 1979). They also showed a correlation ($p < 0.05$) with data from Mettnau on the Bodensee (Bairlein 1981). The weak correlations found between Falsterbo and Ottenby, and between Falsterbo and Hammarön (Svensson 1981), disappeared when data from more years were added.

CORRELATIONS BETWEEN RINGING FIGURES AND POPULATION DENSITY

As seen from Fig. 1a, there is a positive relationship between an Estonian population index based on large numbers of Great Tits in nestboxes (H. Vilbaste in litt.) and the number of Great Tits ringed

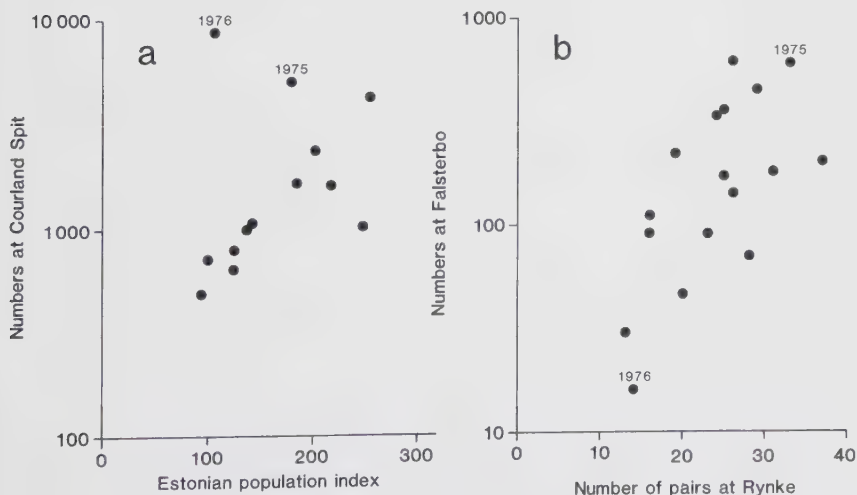


Fig. 1. The relation between breeding population density of the Great Tit and the numbers ringed on migration the following autumn at Courland Spit (a) and at Falsterbo (b).

at Courland Spit when one excludes 1975 and 1976 ($p < 0.01$). These are exactly those two years when large numbers of Great Tits crossed the Baltic. It seems likely that larger than usual numbers of tits were concentrated to the eastern Baltic coast under the meteorological conditions that prevailed in October in these years. Also the limited material from Pape shows a statistically significant correlation with the Estonian index ($p < 0.05$). There is an even better correlation between the numbers ringed at Falsterbo and the population density in a nestbox area some 70 km to the north-east (Fig. 1b; data from Sten Svensson in litt.). It has been claimed (e.g., Alerstam 1982) that, in autumn 1975, Falsterbo was heavily invaded by tits of an easterly origin, whereas the influx across the Baltic in 1976 had no influence there. It is true that a Great Tit ringed at Rybachi was captured at Falsterbo in October 1975 (Roos 1983), but the points for the two years do not deviate in any obvious way from those for the rest of the period.

Also in the Blue Tit there is a correlation between population density and numbers caught at Falsterbo. Thus, Svensson (1981) obtained a highly significant correlation ($p < 0.001$) with a population index, calculated on data from several census areas in South and South Central Sweden, when he excluded 1976. The point for that year fell far to the right of the regression line, and Svensson suggested that this could be explained by the tits staying in the beech forests of South Sweden to exploit that year's extremely rich beech mast crop, in accordance with Ulfstrand's (1962) hypothesis. It seems more likely, however, that the deviation was caused by a bias in the population index, where localities in South Central Sweden dominated (Svensson pers. comm.); whereas the Blue Tit population, according to our data, decreased dramatically (by 52-82 %) between 1975 and 1976 in six nestbox areas in southern Sweden and reached a deep low in 1976, it remained at about the same level, or decreased very little, in seven others further north. Probably the same applies to the Great Tit, where Svensson's index value for 1976 likewise is high compared to our figures (see Svensson 1981, Fig. 4).

Both in the Great and the Blue Tit, the correlation coefficients for the relationship between density and numbers caught at Falsterbo were highest for the populations closest to the observatory. This may indicate that the tits caught at Falsterbo mainly originate from southernmost Sweden. There were, however, some statistically significant, or nearly significant, correlations also with populations further north, in South Central Sweden, particularly in the Blue Tit.

In this species, proportionally more of the recoveries involve long-distance movements (Källander in press).

DISCUSSION

The idea that population density is a proximate factor for migratory movements of tits is far from new. Already Kluijver (1951) suggested that emigration was density dependent, and that, in years when populations peaked synchronously over large areas, eruptive migrations would result. He also looked for a correlation between years of high population density in his study area (Oranje Nassau's Oord) and published reports of mass movements, but without finding any such relationship. Also Ulfstrand (1962) regarded population density as the proximate factor that started 'irruptions', while Cramp (1963) found it to be the main causative factor.

Berndt & Henss (1963, 1967) pointed out that population maxima of Great and Blue Tits in their study areas at Braunschweig coincided with peak numbers at Falsterbo and stressed the importance of density as a cause of large-scale 'irruptions'. Observing that almost all large decreases in tit numbers occurred after heavy emigrations, they drew the group-selectionist conclusion that emigration had evolved because it had 'eine arterhaltungsbegünstigende Funktion'. Similar correlations between high population densities and autumn movements were also established in the Siberian Tit Parus cinctus and the Long-tailed Tit Aegithalos caudatus (Hildén 1968, 1977).

The poor agreement between bird observatories with regard to fluctuations in the number of tits ringed each year (Ehrenroth 1976, this study) suggests that, to a large extent, these numbers are determined by population fluctuations on a local or regional scale. Some population peaks coincide over large areas (van Balen, Hildén, Källander & Schmidt in prep.), but the series of data from the various bird observatories do not overlap enough to show to what extent they are reflected in synchronous fluctuations in ringing numbers, as they would be expected to be.

Ulfstrand (1962) concluded that, although proximately triggered by high densities, the 'irruptive' movements of Great and Blue Tits were governed by the size of beech mast crop in autumn; in years rich in mast the tits would stay and winter in southernmost Sweden, in poor mast years irruptions would take place. Perrins (1966) pointed out the difficulty in separating the effects of density and

beechmast; survival is good in years when mast is plentiful (not necessarily an effect of mast being used as winter food; see discussion in Perrins (1980)), resulting in dense populations in the year following a rich crop. Since the beech does not fruit two years in succession, high population levels and poor crops tend to coincide. Because the strength of migration seems to be correlated with population densities also in areas outside the distribution range of the beech (e.g., Estonia), clearly the beech mast crop cannot be a decisive factor of whether migration takes place or not. However, it could have an influence on the length of the migratory movements.

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REFERENCES

- Alerstam, T. 1982. Fågelflyttning. Lund: Signum.
- Bairlein, F. Ökosystemanalyse der Rastplätze von Zugvögeln: Beschreibung und Deutung der Verteilungsmuster von ziehenden Kleinvögeln in verschiedenen Biotopen der Stationen des „Mettnau-Reit-Ilmlitz-Programmes“. Ökologie der Vögel 3: 7-137.
- Berndt, R. & Henss, M. 1963. Die Blaumeise, Parus c. caeruleus L., als Invasionsvogel. Vogelwarte 22: 93-100.
- Berndt, R. & Henss, M. 1967. Die Kohlmeise, Parus major, als Invasionsvogel. Vogelwarte 24: 17-37.
- Borgström, E. In press. (The influence of extreme weather conditions in the summer of 1981 on the production of fledglings in some species breeding in nestboxes.) Vår Fågelv. (In Swedish with summary in English.)
- Cramp, S. 1963. Movements of tits in Europe in 1959 and after. Brit. Birds 56: 237-263.
- Dolnik, V.R. & Paevski, V.A. 1979. (Dynamics of Baltic bird populations in 1960-1976.) Ekologia 10: 59-69.
- Ehrenroth, B. 1976. (Movements of tits Paridae at Hammarön in northern Lake Vänern.) Vår Fågelv. 35: 261-278. (In Swedish with summary in English.)
- Frelin, C. 1975. Comportement invasionnel des Mésanges noires (Parus ater) et espèces apparentées, au Col de La Golèze en 1972. L'Oiseau et R.F.O. 45: 41-64.
- Frelin, C. & Martinet, M. 1975. Migrations de la Mésange charbonnière Parus major au Col de La Golèze (Haute-Savoie). Alauda 43: 203-215.
- Hildén, O. 1968. Die Invasion der Lapplandmeise, Parus cinctus, in Finland 1963/64. Vogelwarte 24: 189-198.

- Hildén, O. 1977. Mass irruption of Long-tailed Tits Aegithalos caudatus in northern Europe in 1973. Ornis Fennica 54: 47-65.
- Hjorth, C., Lindholm, C.-G. & Pettersson, J. 1981. (Bird ringing statistics at Ottenby Bird Observatory 1946-1980.) Rapport från Ottenby fågelstation nr 2.
- Källander, H. In press. (Recoveries of Great Tits Parus major and Blue Tits P. caeruleus ringed in Sweden.) Vår Fågelv. (In Swedish with summary in English.)
- Kluijver, H.N. 1951. The population ecology of the Great Tit, Parus m. major L. Ardea 39: 1-135.
- Lack, D. 1966. Population Studies of Birds. Oxford: Clarendon Press.
- Lindholm, C.-G. 1978. (The migration of the great tit Parus major across the Baltic Sea in the autumns of 1975 and 1976.) Anser, Suppl. 3. (In Swedish with summary in English.)
- Lindskog, H. & Roos, G. 1979. (The autumn migration of blue tits Parus caeruleus and great tits Parus major at Falsterbo in 1973-78.) Anser 18: 171-188. (In Swedish with summary in English.)
- Lipsbergs, J. & Rute, J. 1975. (Autumn migration of tits of the family Paridae and the Long-tailed Tit on the south-west coast of Latvia in 1967-1971.) Comm. Baltic Commission Study Bird Migr. 9: 105-122. (In Russian with summary in English.)
- Odintsova, N. 1975. (Character of the tits migration on the Courish Spit in 1957-1966.) Comm. Baltic Commission Study Bird Migr. 9: 91-104. (In Russian with summary in English.)
- Perrins, C.M. 1966. The effect of beech crops on Great Tit populations and movements. Brit. Birds 59: 419-432.
- Perrins, C.M. 1980. Survival of young Great Tits, Parus major. Acta XVII Congr. Int. Orn. Berlin: 159-174.
- Roos, G. 1983. (Migration, wintering, and longevity of birds ringed at Falsterbo in 1947-1980.) Anser, Suppl. 13. (In Swedish with summary in English.)
- von Schantz, T. 1981. Evolution of group living, and the importance of food and social organization in population regulation; a study of the red fox (Vulpes vulpes). Doctoral thesis, Univ. of Lund.
- Svensson, S. 1981. (Population fluctuations in tits Parus, Nuthatch Sitta europaea, and Treecreeper Certhia familiaris in South Sweden.) Proc. Second Nordic Congr. Ornithol. 1979: 9-18.

Återfynd av talgoxar och blåmesar ringmärkta i Sverige

HANS KÄLLANDER

Vissa höstar utgör talgoxar och blåmesar ett ganska markant inslag på våra sträcklokaler. Vid Falsterbo har höstetid drygt 7 000 talgoxar och 28 000 blåmesar noterats utsträckande (Ulfstrand m.fl. 1974, Roos & Lindskog 1979). Varifrån rekryteras dessa mesar? Vart tar de vägen? Vilka andra rörelser företar mesarna?

I denna uppsats analyserar jag ringåterfynd av svenskmarkta talgoxar och blåmesar. Jag har härvid begränsat mig till fynd mer än cirka 50 km från märkplatsen. Återfynd av mesar märkta i Sverige, Norge och Finland har tidigare bearbetats av Rendahl (1959). I denna uppsats använder jag på nytt en stor del av de återfynd han redovisade. Detta görs för att uppnå en så fullständig bild som möjligt. Vidare har jag utnyttjat de återfynd Ringmärkningscentralen publicerat i sina rapporter för perioden 1960–1971 (Österlöf 1964 och följ.). Återfynd efter 1971 har vänligen ställts till mitt förfogande av Ringmärkningscentralen. Uppsatsen omfattar fynd rapporterade t.o.m. 1982.

Den kategoriindelning av återfynden jag gjort skiljer sig en del från den Rendahl (1959) tillämpade. Indelningsgrunderna kan givetvis alltid diskuteras, liksom man nästan aldrig kan undvika besvärliga gränsfall. En fågel märkt i början av mars kan t.ex. fortfarande befinna sig på vinterkvarter, eller den kan ha påbörjat sitt sträck från detta.

För fåglar fångade vid Falsterbo redogör Roos (1983). Jag har här endast tagit upp kompletterande fynd, huvudsakligen gjorda efter 1980, som utgör slutåret i Roos sammanställning.

Den följande resultatdelen består huvudsakligen av kommentarer till en serie kartor, där återfynden prickats in. På sedvanligt sätt har märkplats och återfyndsplats förbundits med en rät linje. Återfyndslokalen representeras av den ände av linjen, vid vilken en siffra återfinnes (undantag figur 9c). Denna siffra svarar mot uppgifter i figur- eller appendix-text.

Talgoxe

Återfynd av fåglar märkta som boungar

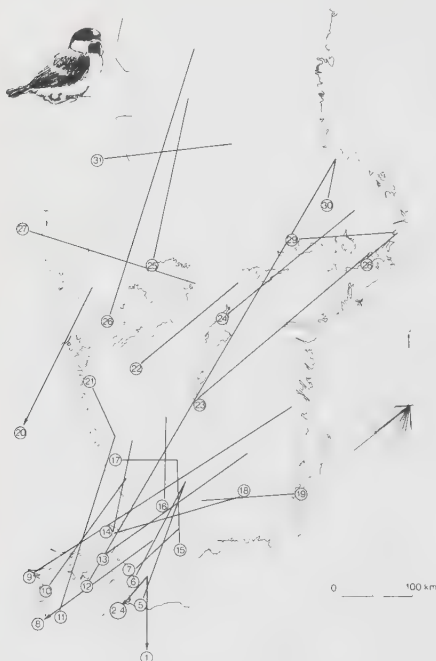
Återfynd av talgoxar märkta som boungar i den södra hälften av Sverige och återfunna den närmast följande vintern och våren har lagts in i figur 1, medan sådana som återfunnits först senare, dvs efter mer än 12 månader, återfinns i figur 2. För norrlandsmärkta talgoxar har båda kategorierna sammanförts i figur 3.

Vad gäller återfynden närmast efter märkningen (figur 1) har som synes endast två av de sydsvenska talgoxarna rört sig i östliga riktningar, övriga inom syd-nordväst. Majoriteten av återfynden (60%) faller inom sydvästsektorn. Mönstret är någorlunda likartat för de talgoxar som märkts i norra Sverige (figur 3). Av dessa har dock fyra (av 12) rört sig västerut mot den norska kusten. Flertalet talgoxar har tillryggelagt mätliga sträckor. Medianavståndet (för sådana som förflyttat sig mer än cirka 50 km) är ungefär 155 km för talgoxar såväl från den södra som från den norra halvan av landet. Enstaka fåglar har dock rört sig avsevärt längre distanser, framför allt nr 12 i figur 1 (cirka 600 km).

För boungemärkta talgoxar som återfunnits efter 1 år eller mer (figur 2, 3) är bilden mera splittrad; lång-återfynd föreligger från platser såväl norr som söder om märkort, med viss översikt för de förra i det sydsvenska materialet. Det är svårt att veta hur dessa fynd skall tolkas. Har förflyttningen skett under den första levnadshösten (alternativt som ett återsträck efter den första övervintringen) eller har den skett senare? Fynden nr 4, 17, 18, 20 och 21 (figur 2), som samtliga är fynd från andra vintern, kan indikera sträck söderut under andra levnadshösten – i medeltal är 9 % av de talgoxar som höstetid fångas vid Falsterbo mer än 1 år gamla (Lindskog & Roos 1979, G. Roos i brev).

Ett av fynden är mycket märkligt (nr 21). Fågeln märktes den 5 juni 1972 i Åsbo, Östergötland, och rapporterades funnen död i Schweiz kring den 10 maj 1977, alltså 5 år efter märkningstillfället. Förutom att det innebär en ovanligt hög livslängd – ehuru inte extrem, se Edeltam & Österlöf (1969), Perrins (1979) – utgör det den svenska talgoxmärkningens sydligaste återfynd. Eftersom det är ensamt i sitt slag kan det vara befogat att åtminstone tills vidare inte tillmäta fyndet alltför stor betydelse.

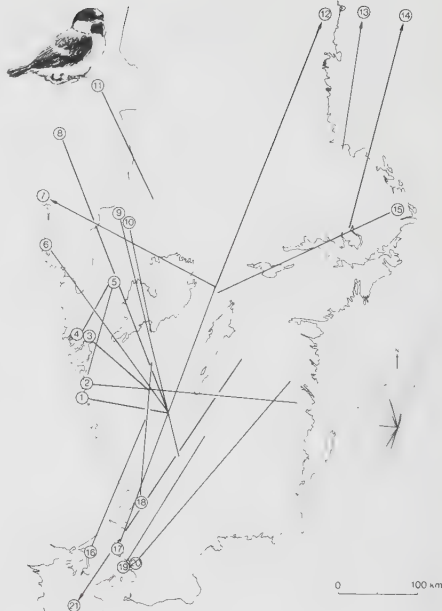
Medianavståndet mellan märk- och fyndplats är, oavsett region, cirka 200 km och längsta avstånd, bortsett från fyndet i Schweiz, cirka 700 km.



Figur 1. Talgoxar märkta som boungar i södra halvan av Sverige och återfunna närmast följande höst-vinter. Numreringen avser fyndlokaler. Endast fynddatum och fyndort anges. Parentes anger att datum är osäkert. I denna och i följande figurer markerar cirkeln i den inlagda "sträckrosen" 200 km avstånd från märkplatsen.

Great Tits ringed as nestlings in the southern half of Sweden and recovered in the following autumn and winter. Numbers refer to the place of recovery. Brackets indicate that date is uncertain. In this and the following figures, the circle in the inserted diagram that shows direction of movements denotes 200 km from the place of ringing.

1 = 28 jan, Greifswald, DDR; 2 = 29 sep, Falsterbo; 3 = 5 okt, Falsterbo; 4 = 13 okt, Falsterbo; 5 = 10 okt, Alstad, Sk; 6 = (7 nov), Borgeby, Sk; 7 = 9 nov, V. Karaby, Sk; 8 = 2 feb, Heide, Holstein, BRD; 9 = (2 jan), Rösnes, Sjöland, Danmark; 10 = 26 jan, Ruds Vedby, Sjöland, Danmark; 11 = 5 nov, Fuglebjærg, Sjöland, Danmark; 12 = 24 nov, Roskilde, Sjöland, Danmark; 13 = 7 nov, Fredensborg, Sjöland, Danmark; 14 = 29 jan, Strandbaden, Sk; 15 = 21 april, Ignaberga, Sk; 16 = 2 nov, Hinneryd, Sm; 17 = 16 feb, Köinge, Hl; 18 = 5 dec, Linneryd, Sm; 19 = okt, Kalmar, Sm; 20 = 25 feb, Ulsted, Jylland, Danmark; 21 = 8 apr, Kungälv, Boh; 22 = 21 jan, Vedum, Vg; 23 = 28 feb, Huskvarna, Sm; 24 = 1 nov, Hammar, Nrk; 25 = 4 okt, Nor, Vg; 26 = 18 jan, Dalskog, Dls; 27 = 28 nov, Drammen, Norge; 28 = 4 feb, Stockholm; 29 = (5 feb), Västerås, Vstm; 30 = (3 feb), Harbo, Upl; 31 = 5 nov, Hof, Solör, Hedmark, Norge;



Figur 2. Talgoxar märkta som boungar samt som juvenila under sommaren (senast 15 augusti) i södra halvan av Sverige och återfunna mer än 1 år senare. Ungefärligt antal månader mellan märkning och fynd anges, eljest som i figur 1.

Great Tits ringed as nestlings or as fledglings before 15 August in the southern half of Sweden and recovered more than 1 year later. Approx. no. of months between ringing and recovery also indicated, else as in Fig. 1.

1 = 24 okt, Göteborg (16 mån); 2 = 13 nov, Kungälv, Boh (17 mån); 3 = 23 feb, Uddevalla, Boh (32 mån); 4 = 16 sep, Munkedal, Boh (15 mån); 5 = 14 apr, Billingsfors, Dls (70 mån); 6 = 20 mar, Råde, Östfold, Norge (33 mån); 7 = 23 nov, Guddal, Sogn og Fjordane, Norge (17 mån); 8 = (16 jan), Skreia, Oppland, Norge (18 mån); 9 = 3 maj, Åmotsfors, Vrm (23 mån, häckande); 10 = 9 feb, Arvika, Vrm (44 mån); 11 = 28 okt, Osen, Österdalen, Hedmark, Norge (15 mån); 12 = (20 nov), Norsjö, Vb (18 mån); 13 = 8 dec, Glommerstråk, Plpm (16 mån); 14 = 6 nov, Överklinten, Vb (15 mån); 15 = 6 okt, Erken, Upl (16 mån); 16 = 8 jan, Ramlöse, Sjöland, Danmark (19 mån); 17 = 25 okt, Helsingborg, Sk (16 mån); 18 = 11 jul, Tönnersjö, Hl (36 mån); 19 = (1 okt), Landskrona, Sk (16 mån); 20 = 20 dec, Svalöv, Sk (16 mån); 21 = Belfaux (46.49 N, 07.06 E) Schweiz (59 mån).



Figur 3. Talgoxar märkta som boungar i den norra halvan av Sverige och återfunna närmast följande höstvintr (nr 1–14) respektive efter mer än 1 år (nr 15–24). För de senare ges ungefärligt antal månader mellan märk- och fynddatum.

Great Tits ringed as nestlings in the northern half of Sweden and recovered the following autumn and winter (nos. 1–14), or after more than 1 year (nos. 15–24). For the latter, the approx. no. of months between ringing and recovery is given.

1 = 30 nov, Delsbo, Hls; 2 = 30 dec, Färila, Hls; 3 = (21 nov), Nord-Odal, Hedmark, Norge; 4 = slutet av nov, Kvenvaer, Hitra, Norge; 5 = 8 mar, Snåsa, Norge; 6 = 29 mar, Grundfors, Ås lpm; 7 = (20 okt), Volgsjöfors, Ås lpm; 8 = (22 dec), Bleikvassli, Nordland, Norge; 9 = 10 dec, Luktvatn, N Mosjøen, Nordland, Norge; 10 = 7 jan, Svanström, Vb; 11 = 22 okt, Kvickjokk, Lu lpm; 12 = 28 dec, Hakkasbyn, Lu lpm; 13 = 9 nov, Gunnarsbyn, Nb; 14 = 13 nov, Maksniemi, Kemi, Finland; 15 = 26 mar, Skorped, Åg (21 mån); 16 = 13 okt, Örebro, Åg (15 mån); 17 = 29 dec, Granäsby, Ås lpm (29 mån); 18 = 15 jan, Marsvik, Ås lpm (65 mån); 19 = nov, Bleikvassli, Nordland, Norge (16 mån); 20 = 25 apr, Ytterien, Mo, Norra Helgeland, Norge (21 mån); 21 = 19 apr, Hortlax, Nb (21 mån); 22 = 8 maj, Killingi-Fjällåsen, Lu lpm (46 mån); 23 = nov, Kersilö, Sodankylä, Finland (17 mån); 24 = 20 jul, Pyhäjärvi, Pelkosenniemi, Finland (13 mån).

Återfynd av talgoxar märkta vintertid

Talgoxar märkta vintertid (nov–feb) i södra halvan av Sverige och återfunna under våren och sommaren efter märkningen redovisas i figur 4 och sådana som åter-



Figur 4. Talgoxar märkta på troliga vinterkvarter i södra halvan av Sverige (nov–feb, nr 1–6) samt märkta på troligt vårsträck (A–D) och återfunna följande vår–sommar. Dessutom har fem i Sverige under våren återfunna talgoxar, vilka ringmärkts i Danmark den föregående vintern lagts in (från Hansen 1978). För fåglar märkta på vinterkvarter ges endast fynddata.

Great Tits ringed in presumed winter quarters in the southern half of Sweden (Nov.–Feb. nos. 1–6), and probably on migration (A–D), and recovered the following spring or summer. In addition five records of birds ringed in Denmark in winter and recovered in Sweden are plotted (from Hansen 1978).

1 = 3 maj, Sörfjord, Engan, Nordland, Norge; 2 = (21 juli), Bognes, Tysfjord, Nordland, Norge; 3 = (2 apr), Heby, Runhällen, Vstm; 4 = (8 apr), Enköping, Upl; 5 = 13 jul, Örebro, Nrk; 6 = 6 jun, Aneboda, Sm; A = märkt Falsterbo 31 mars 1981, kontr. Christiansø, Danmark 4 april; B = märkt Utklippan 9 april 1981, kontr. Sundre, Gtl 21 maj, troligen häckande; C = märkt Torna-Hällestad 15 mars 1974, funnen död Gärsnäs, Sm 31 mars; D = märkt Nyköping 19 mars 1976, kontr. Lågsjär, Finland 8 april.

funnits senare i figur 5. I figur 4 har inkluderats fem fåglar märkta i Danmark och återfunna i södra Sverige (Hansen 1978). Dessutom ingår fyra fåglar märkta



Figur 5. Talgöxar märkta på troliga vinterkvarter i södra halvan av Sverige (nov–feb, nr 1–26) samt märkta på troligt vårstreck (A–D) och återfunna följande höst eller senare. Inom parentes anges ungefärligt antal månader mellan märkning och återfynd.

Great Tits ringed in presumed winter quarters in the southern half of Sweden (Nov–Feb, nos. 1–26) together with four birds probably on spring migration (A–D). The number of months between ringing and recovery in brackets.

1 = 2 maj, Östby, Trysil, Hedmark, Norge (40 mån); 2 = 26 jan, Straumbygd, V Mo i Rana, Nordland, Norge (44 mån); 3 = 20 okt, Korskrogen, Hls (36 mån); 4 = 7 feb, Bergnäs, 38 km NV Sorsele, Ly lpm (24 mån); 5 = (7 nov), Storbrennan, Sättna, Mpd (32 mån); 6 = 2 feb, Svappavaara, To lpm (12 mån); 7 = 3 feb, Oksfjordhamn, Nord-Troms, Norge (24 mån); 8 = 27 feb, Krylbo, Dlr (15 mån); 9 = 3 okt, Skogs-Tibble, Brønna, Upl (8 mån); 10 = Söndre Langåra, Frogn, Akershus, Norge (12 mån); 11 = (8 feb), Fåberg, Opland, Norge (47 mån); 12 = 9 apr, Rörkiven, Nössemark, Dls (15 mån); 13 = 9 jun, Stockholm (77 mån); 14 = 7 nov, Ekesjö, Ög (11 mån); 15 = 10 feb, Derrenäs, Frändefors, Dls (22 mån); 16 = 15 mar, Sundals Ryr, Dls (26 mån); 17 = 7 jan, Norslätt, Säve, Boh (13 mån); 18 = 20–30 nov, Brandsbo, Ödenäs, Vg (12 mån); 19 = 19 feb, Sjöbo, Borås, Vg (10 mån; märkt 13 apr, således ev på vårstreck); 20 = 30 nov, Björstorp, Ljungsarp, Vg (9 mån); 21 = 5 jan, Björksäter, Forserum, Sm (50 mån); 22 = 30 nov, Nässjö, Sm (11 mån); 23 = (21 nov), Husnäs, Karlstorp, Sm (10 mån); 24 = 4 mar, Hinnakull, Torup, Hl (13 mån); 25 = 5 okt, trakten av Ljungby, Sm (8 mån); 26 = 15 jun, Trummenäs, Karlskrona, Bl (30 mån); A = 15 okt, Mariestad, Vg (18 mån); B = 31 okt, 22 km S Alfva, Hls (7 mån); C = ?, Taveljö, Vb (cirka 2 år efter märkningen); D = apr, Suurmäki, Mikkeli, Finland (12 mån).



Figur 6. Talgöxar märkta på troliga vinterkvarter i norra halvan av Sverige (tillsammans med fyra fåglar märkta under tänkbar sträcktid, 10 okt–3 nov, markerade A–D). Heldragen linje avser fåglar återfunna följande vår–sommar, streckad linje fåglar återfunna senare. För dessa anges ungefärligt antal månader mellan märk- och fynddatum.

Great Tits ringed in presumed winter quarters in the northern half of Sweden (together with four birds ringed on possible migration, 10 Oct–3 Nov., indicated A–D). Unbroken lines refer to birds recovered in the following spring and summer, broken lines to birds recovered later. For the latter approx. no. of months between ringing and recovery is given.

1 = (28 apr), Akkapakte, Arjeplog, Pi lpm; 2 = (1 maj), Lövänger, Vb; 3 = 27 apr, Vändtrask, Nb; 4 = 30 jun, Övertorneå, Nb; 5 = Björånes, Stor-Elvdal, Hedmark, Norge (22 mån); 6 = (11 jan), Seierstad, Fosnes, Nord-Trøndelag, Norge (11 mån); 7 = 27 nov, Borgafjäll, Ås lpm (7 mån); 8 = (3 nov), Elvegård, Nordland, Norge (12 mån); 9 = 29 sep, Volgsjöfjäll, Ås lpm (21 mån); 10 = (10 okt), Kamsjön, Vindeln, Vb (7 mån); 11 = 17 okt, Skrämråsk, Vb (9 mån); 12 = (26 mar), Kusmark, Vb (15 mån); 13 = 5 nov, Yttersta, Nb (21 mån); 14 = (18 dec), Vallsjärn, Nb (12 mån); A = 14 dec, Naevernes, Velfjord, Nordland, Norge (25 mån); B = 25 okt, Mjösjöby, Vb (12 mån); C = (15 nov), Bjurholm, Ång (13 mån); D = 4 nov, Gällivare (11 dagar).

under troligt vårsträck. För talgoxar märkta i norra halvan av Sverige har båda kategorierna återfynd sammanförts i figur 6.

Fyndmönstret är ganska likartat i samtliga fall: fynden ligger med blott ett par undantag norr om märkplatsen, dvs indikerar ett återsträck från en sydligare belägen övervintringsplats. Bland dem finns ett antal verkliga långdistansrörelser. Nr 1 och 2 i figur 4, märkta i Örebro respektive Göteborg, är återfunna följande sommar i Nordlands fylke i Norge, cirka 1 000 km norr om den troliga övervintringslokalen. Nr 2, 4, 6 och 7 i figur 5 är likaledes återfunna långt norrut, samtliga vintertid, 1–4 år efter märkningen. Detta innebär troligen att de tillbragt sin första vinter på lokaler i södra och mellersta Sverige, medan de stannat på eller nära häckplatsen följande vinter/vintrar.

Medianavståndet mellan märk- och fyndplats är cirka 150 km för talgoxar återfunna vår och sommar efter märkningen, 220 km för sådana som återfunnits senare, dvs ungefär samma skillnad som för boungemärkta fåglar återfunna första säsongen respektive senare.

Återfynd av talgoxar märkta under sträcktid om hösten

I figur 7 a–d redovisas fynd av talgoxar märkta i södra Sverige under perioden september–oktober. De fynd som listas i tabell 1 har dock ej medtagits. Fullständiga fynddata återfinnes i appendix 1. De talgoxar som märkts i Norrland under motsvarande period är inkluderade i figur 6.

Ser man först på de talgoxar som återfunnits under hösten och vintern (våren) efter märkningen (heldragna linjer), så återfinns nära hälften av fynden inom sydväst-kvadranten. Några fynd avviker dock. Nr 14 i figur 7a

representerar uppenbarligen en fågel som återvänt till sin ursprungstrakt i Estland, där den kontrollerades den 31 mars. Också nr 6 utgör ett värfynd. Men även nr 5 och 6 i figur 7a, nr 5 i b, 8 och 12 i c, samt nr 9 i d, representerar talgoxar som flugit norrut i förhållande till märkplatsen. Det kan röra sig om fåglar som aldrig sträckt ut i den "normala" sträckriktningen utan retursträckt.

Fynd nr 9 i figur 7a representerar ett långfynd av samma karaktär som nr 12 i figur 1a, dvs en talgoxe märkt i Svealand och återfunnen på Själland. Den ringmärktes på Svenska Högarna den 28 september 1981 och kontrollerades, fortfarande på vinterkvarter, eller, troligare, på vårsträck vid Gilbjerg Hoved den 28 mars 1982. De två resterande fynden av Svenska Högarna-märkta talgoxar ligger i nordvästkvadranten. De kan representera fåglar från Balticum som hamnat på en nordvästlig kurs; talgoxar från Estland har kontrollerats såväl på Svenska Högarna som på de åländska sträckstationerna (Pettersson 1981, t.ex. Kastepold & Kabal 1977).

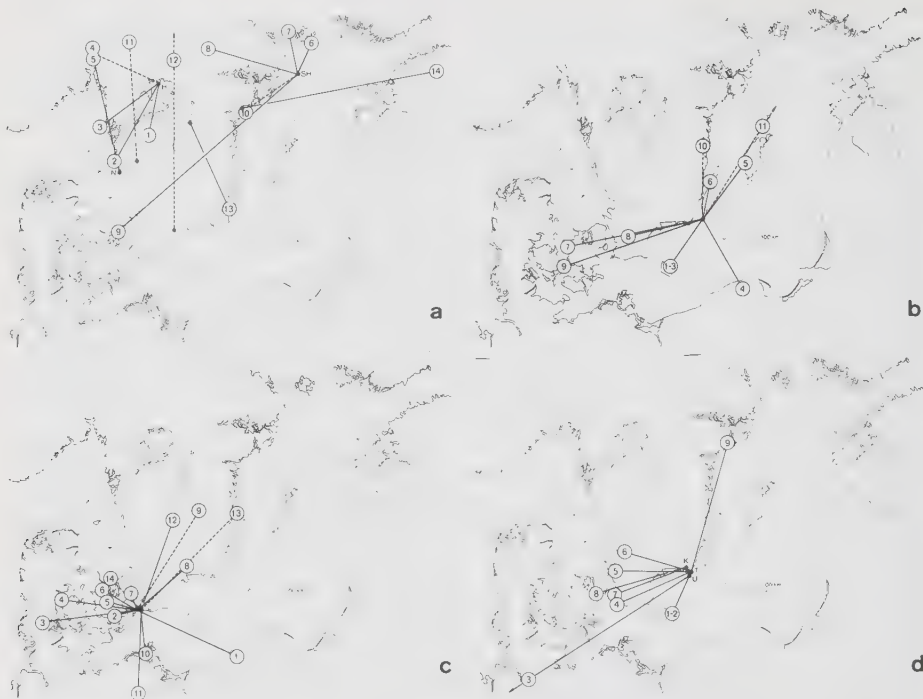
Fynden av Falsterbo-märkta talgoxar stämmer utmärkt överens med dem Roos (1983) redovisar, dvs majoriteten av de talgoxar som passerar ut vid Falsterbo tycks avbryta sträcket i huvudsak redan på Själland och de danska öarna.

Utklippan står för ett av de få långfynd som gjorts på Kontinenten (nr 3, figur 7d). Fågeln återfanns 42 dagar efter märkningen vid Zoutleeuw i norra Belgien, ungefär 850 km mot sydväst. Med tanke på att baltiska talgoxar fångats på Torhamn och Utklippan (Lindholm 1978) och förefaller sträcka längre än svenska talgoxar (Alerstam 1982, van Balen & Speek 1976), kan det inte uteslutas att det rör sig om en fågel från den östra sidan av Östersjön.

Tabell 1. Talgoxar märkta på höststräck vid svenska fågelstationer och återfunna eller kontrollerade i Balticum följande höst, respektive talgoxar märkta på vårsträck vid Ottenby återfunna följande höst vinter.

Great Tits ringed on autumn migration at Swedish bird observatories and controlled or recovered in the Soviet Baltic republics the following autumn together with three Great Tits ringed on spring migration at Ottenby and recovered the following autumn or winter.

1. 2 558 792	1K ♂ 76.10.22	Torhamn	v	77.10.22	Pape (56.09 N, 21.02 E)
2. 2 595 339	1K ♀ 76.10.23	Ottenby	x	77.09.23	Valmiera (57.30 N, 25.25 E)
3. 2 595 447	2K+ ♀ 76.10.24	ibidem	v	78.10.20	Pape
4. 2 612 549	1K ♀ 77.10.10	ibidem	x	78.10.20	ibidem
5. 2 682 567	1K ♂ 79.10.17	Hartsö- Enskär	v	80.10.25	ibidem
6. 2 095 697	1K+ 63.04.09	Ottenby	x	64.10.16	Perstorp (56.08 N, 13.24 E)
7. 2 095 772	1K+ 63.04.12	ibidem	x	64.02.20	Clausthal-Zellerfeld (51.48 N, 10.20 E)
8. 2 772 707	2K ♀	ibidem	v	81.10.06	Falsterbo (55.23 N, 12.50 E)



Figur 7. Talgoxar märkta under sträcktid (15 sep–30 okt) i södra halvan av Sverige och återfunna samma höst eller närmast följande vinter och vår (heldragna linjer) respektive återfunna påföljande höst eller senare (streckade linjer). Fullständiga data i appendix 1. (a) = talgoxar märkta vid Hammarön (H), Nidingen (N), Svenska Högarna (SH) samt på ytterligare några platser i södra Sverige; (b) = talgoxar märkta på Ottenby; (c) = talgoxar märkta vid Falsterbo (F), utöver dem som redovisas av Roos (1983), samt vid Ljunghusen (L); (d) = talgoxar märkta på Torhamn (T), Utklippan (U) och i Karlskrona (K).

Great Tits ringed during the autumn migration period (15 Sep–30 Okt) in the southern half of Sweden and recovered in the same autumn, the following winter, or spring (unbroken lines), or in the following autumn or later (broken lines). Ringing and recovery data in appendix 1. (a) = ringed at Hammarön (H), Nidingen (N), Svenska Högarna (SH) bird observatories and in a few other places in South Sweden; (b) = ringed at Ottenby; (c) = ringed at Falsterbo (F), except those listed by Roos (1983) and at nearby Ljunghusen (L); (d) = ringed at Torhamn (T) and Utklippan (U) bird observatories, and at Karlskrona (K).

De fynd som gjorts mer än 1 år efter märkningen ligger alla norr om märkplatsen och liknar i detta avseende den överväldigande majoriteten fynd av vintermärkta. Två avslöjar rörelser över betydande avstånd: en talgoxe märkt i Råbelöv i nordöstra Skåne återfanns drygt 3 år senare vid Moldfjord i norra Norge, drygt 1200 km norr om märkplatsen (figur 7a, nr 12), och en Ottenby-märkt hittades följande höst vid Iitti i södra Finland, cirka 800 km mot nordost (figur 7b, nr 11).

En del märkningar vid svenska fågelstationer visar att åtminstone vissa talgoxar återvänt till Balticum, där de uppenbarligen deltagit i sträck också följande höst (tabell 1, nr 1–5). Beträffande de vårmärkta (nr 6–8) är det naturligtvis mera osäkert var de uppehållit sig mellan märknings- och återfyndstillfällena. Andelen talgoxar som deltar i sträckrörelser under sitt andra levnadsår eller senare tycks eljest inte vara högre i de baltiska populationerna (Lipsberg & Rute 1975, Efremov 1975) än exempelvis vid Falsterbo (Lindskog & Roos 1979).



Figur 8. Blåmesar märkta som bouncar (i två fall juv märkta i början av aug. nr 3 och 14) och återfunna följande höst och vinter (nr 1–22, heldragna linjer) respektive efter 1 år eller mer (nr 23–30, streckade linjer). För de senare anges ungefärligt antal månader mellan märkning och återfynd.

Blue Tits ringed as nestlings (in two cases as fledglings in early August) and recovered the following autumn or winter (nos. 1–22, unbroken lines) and after 1 year or more (nos. 23–30, broken lines). For the latter approx. no. of months between ringing and recovery is given in brackets.

1 = 4 jan, Samsö, Danmark; 2 = 13 okt, Skanör; 3 = 16 okt, Falsterbo; 4 = 17 okt, Falsterbo; 5 = 31 okt, Håkøpinge; 6 = "sommaren", Skromberga (fyndet rapporterat ett år senare); 7 = 25 sep, Smygehuk; 8 = 6 okt, Smygehuk; 9 = (29 dec); Eslöv; 10 = 14 okt, Ottenby; 11 = 10 okt, Brötterspören; 12 = 3 okt, Hoburgen; 13 = 12 okt, Hoburgen; 14 = 31 dec, Morup och 4 mar, Långås; 15 = 12 feb, Brötjemark; 16 = 9 okt, Jomfrulund (58.52 N, 09.36 E); 17 = 18 jan, Papper, Hvaler, Norge; 18 = 21 okt, Horten, Norge; 19 = 9 jan, 7 km N Hønefoss, Norge; 20 = 18 okt, Hammarön; 21 = 22 okt, Hammarön; 22 = (20 jan), Sägmyra; 23 = 25 mar, Vallensbäck (45 mån); 24 = 1 mar, Backkeskov Strand, Danmark (21 mån); 25 = 16 jun, Göteryd (48 mån); 26 = 6 okt, Christiansö, Danmark (14 mån); 27 = 16 jun, Dalskog (12 mån); 28 = 18 mar, Kila (22 mån); 29 = 10 mar, V Skedvi (21 mån); 30 = 2 dec, Berg, Trysil, Norge (17 mån).

Blåmes

Återfynd av fåglar märkta som bouncar

Fynden av bouncemärkta blåmesar under den första hösten–vintern antyder två huvudsakliga rörelseriktningar, sydväst respektive nordväst (figur 8). De senare utgör ungefär en tredjedel av fynden. Medianavståndet mellan märk- och fyndplats är ungefär detsamma som för bouncemärkta talgoxar, 140 km.

Endast 8 bouncemärkta blåmesar har återfunnits efter mer än 1 år. Åtminstone fynden 23–26 antyder sträckrörelser under andra hösten eller senare höstar – cirka 6% av de blåmesar som sträcker ut vid Falsterbo är mer än 1 år (Lindskog & Roos 1979, G. Roos i brev); alternativt har fåglarna slagit sig ned på platser de nått under sin första höst.

Återfynd av vintermärkta blåmesar

Antalet återfynd av vintermärkta blåmesar är lågt: fem från våren och sommaren efter märkvintern, två mer än 1 år efter märkningen. Av de förra har fyra fåglar förflyttat sig mellan 49 och 107 km mot norr (NV–NO), medan en fågel, märkt som "ad" i Södertälje den 2 december 1962, kontrollerades på Källandsö i Väneren den 20 april 1963 (cirka 265 km VSV). Till dessa kommer en fågel märkt den 4 april, dvs under tänkbar sträcktid, i Nysund i Närke och återfunnen exakt en månad senare i Fellingsbro i Västmanland (76 km NO).

De båda vintermärkta blåmesar som återfunnits mer än 1 år efter märktillfället är båda märkta i Råbelöv, Skåne. Den ena hittades vid Fredrikssund (55.50 N, 12.04 E) i Danmark i januari 36 månader efter märkningen och den andra vid Langen nära Bremerhafen (57.37 N, 8.36 E) i Västyskland den 4 mars 26 månader efter märkningen. I båda fallen rör det sig alltså om fåglar som lämnat Sverige efter att ha övervintrat där åtminstone en gång dessförinnan.

Återfynd av blåmesar märkta under sträcktid om hösten

I figur 9 redovisas återfynd av blåmesar märkta under perioden september–oktober. Detaljerade fynddata ges i appendix 2. Liksom för pullmärkta finns det ett antal fynd från nordvästkvadranten. Det gäller fåglar märkta på Hammarö och Hartsö–Enskär fågelstationer (figur 9a). Särskilt i det senare fallet kan det naturligtvis inte uteslutas att baltiska fåglar är inblandade. Blåmes nr 10 (figur 9a), liksom för övrigt talgoxe nr 8 (figur 7a), är märkta under höstar, då bevisligen stora mängder baltiska mesar korsade Östersjön som ett resultat av speciella väderleksbetingelser (Lindholm 1978). Eljest är riktningarna huvudsakligen sydliga till västliga. Återfynden av Falsterbo-märkta individer (jfr också karta i Roos 1983) ligger på i medeltal avsevärt kortare avstånd än återfynden från andra märkplatser, nämligen på Själland och de danska öarna, vilket antyder att denna region utgör vinterkvarter för flyttande blåmesar i Sydsverige.



Figur 9. Blåmesar märkta under sträcktid (1 sep–25 okt) och återfunna samma höst eller närmast följande vinter och vår (heldragna linjer) respektive återfunna senare (streckade linjer). Fullständiga data i appendix 2. (a) = blåmesar märkta vid Getterön (G), Nidingen (N), Hammarön med Arnön (H), Kvismaren med Assön (K), Hartsö-Enskär (HE) samt ytterligare ett antal platser i södra Sverige; (b) = blåmesar märkta vid Ottenby; (c) = blåmesar märkta vid Torhamn (T) och Utklippan (U) samt (d) blåmesar märkta vid Falsterbo (F), utöver dem Roos (1983) redovisar, och vid Smygehuk (S). För de senare ges inga fynddata.

Blue Tits ringed during the autumn migration period (1 Sep–25 Oct) and recovered in the same autumn, the following winter, or spring (unbroken lines), or later (broken lines). Ringing and recovery data in appendix 2. (a) = birds ringed in different places in South Sweden (capital letters indicate bird observatories), (b) = birds ringed at Ottenby, (c) = birds ringed at Torhamn (T) and Utklippan (U), (d) = birds ringed at Falsterbo (F) and Smygehuk (S); for the latter no details are given.

Tre av fynden, ett samma år och två senare (nr 8, 14 och 15 i figur 9a), dokumenterar långflyttning i sydlig-sydvästlig riktning för fåglar med ursprung i Mellansverige eller längre norrut. Troligen representerar

de båda senare flyttning under den andra levnads-hösten, men detta kan ej fastslås med full säkerhet utifrån fynduppgifterna.

Diskussion

Av denna sammanställning kan man kanske få intrycket av att flyttning är ett dominerande drag hos talgoxe och blåmes. Så är naturligtvis ej fallet, utan endast en mindre andel av bestånden flyttar. Sålunda fann Rendahl (1959) att cirka 85% av återfynden av de talgoxar, som märkts i Sverige under sommaren som boungar eller juvenila, föll inom 10 km från märkplatsen, medan Plattner & Sutter (1946–47) i Schweiz för motsvarande kategori anger 96% inom 50 km. För blåmesen är den andel som förflyttar sig längre sträckor uppenbarligen något högre. Rendahl (1959) anger att 65% av fynden av ungmärkta faller inom 10 km, Berndt & Henss (1963) 68% inom 6 km, och Mohr (1962) 58% inom 50 km. De båda senare undersökningarna avser Tyskland. Från Belgien rapporterar Thielemans & Eyckerman (1975) 69% inom 10 km, och på grundval av schweiziska ringmärkningsrapporter anför samma författare siffran 61% inom 100 km.

Man kan också nära sig problemet på ett annat sätt. Ulfstrand & Högstedt (1976) anslår det häckande beståndet av talgoxe till cirka 6 miljoner par i Sverige och av blåmes till 200 000. Dessa skattningar är givetvis synnerligen osäkra, men anger i vart fall beståndens storleksordning. Höstpopulationerna är avsevärt större. Utnyttjar man ovan angivna siffror för den andel återfynd, som faller inom olika avstånd från ringmärkningsplatsen, finner man, att det totala antalet talgoxar och blåmesar, som höstetid rör sig längre sträckor inte är så imponerande, och att de antal, som registreras på utsträck vid våra fågelstationer, endast utgör hundradelar av procent för talgoxen och kanske ibland någon procent för blåmesen.

Vad säger då återfyndskartorna om de rörelser flyttande talgoxar och blåmesar företagit? Av kartorna över boungemärkta talgoxar (figur 1 och 2) framgår, att den andel, som återfunnits i sydligaste Sverige men haft sitt ursprung längre norrut, i Mellansverige eller norr därom, är mycket ringa. Den övervägande majoriteten härrör från Götaland, de flesta från de sydligare delarna. Eftersom uppgifter om det antal boungar, som märkts inom olika regioner, inte finns tillgängliga, kan man inte omedelbart säga om figurerna speglar det verkliga mönstret – övervikten för talgoxar från den sydligaste regionen kan vara resultatet av en flitigare ringmärkningsverksamhet där. I det avseendet ger de vintermärkta och sträcktidmärkta fåglarna till-

förlitligare information (figur 4–7). Även i dessa kartor dominerar södra Götaland som sannolikt rekryteringsområde för talgoxar märkta i sydligaste Sverige, med ett par fynd i Mellansverige. Intressant är, att ett antal talgoxar med trolig hemort i nordligaste Sverige och Norge, ringmärkts vintertid i Mellansverige och så långt söderut som i Göteborg. Också nr 12 i figur 7 a, märkt höstetid så långt söderut som i Skåne, tillhör denna kategori.

Kartorna över de talgoxar, som ringmärkts i Norrland (figur 3 och 6), antyder rörelser i ganska olika riktningar. Boungemärkta från samma lokal har återfunnits såväl sydväst som sydost om märkplatsen. Några fynd antyder en rörelse ut mot den (mildare) norska kusten. En talgoxe (nr 6, figur 6) ringmärktes en vinter i Jämtland och återfanns följande vinter vid norska kusten. Man skulle väl förmoda, att flertalet norrländska talgoxar vintertid återfinns i byar och större tätorter, men ringmärkningsmaterialet är ännu alldeles för litet för att kunna spegla en sådan typ av flyttning.

Bilden för blåmesen är än mer ofullständig än för talgoxen. Proportionsvis fler fynd har dock gjorts långt från märkplatsen (figur 8 och 9). Till detta kommer en icke obetydlig andel fynd inom nordvästsektorn. Eftersom dessa inte är inskränkta till en viss säsong, får man förmoda, att de inte orsakats av speciella vindförhållanden utan faktiskt avspeglar en tendens hos syd- och mellansvenska blåmesar att söka vinterkvarter i Sydnorge. Men tills vidare måste detta givetvis betraktas som en spekulatio.

Av det här framlagda materialet tvingas man konstatera att Ringmärkningscentralens förbud mot boungemärkning av talgoxe och begränsning av märkningen av flygga mesar varit olycklig. Hos just talgoxen och blåmesen skulle man kunna få fram ytterst detaljerad information om flyttningsvanor och vinterkvarter. Min rekommendation inför framtiden är att RC bör satsa på märkning av dessa arter, och då företrädesvis på märkning av boungar, respektive av vuxna fåglar vintertid. Dessa två kategorier har det särklassigt högsta informationsvärdet.

Ett tack riktas till förre intendenten vid Ringmärkningscentralen, Sten Österlöf, och till Björn Helander, vilka välvilligt ställt återfyndsmaterial till mitt förfogande, till Gunnar Roos, som låtit mig ta del av publicerat material från Falsterbo samt till Göran Högstedt, som läst och kommenterat manuskriptet.

Summary: Recoveries of Great Tits *Parus major* and Blue Tits *P. caeruleus* ringed in Sweden

This paper deals with long-distance recoveries (more than about 50 km from the place of ringing) of Great and Blue Tits ringed in Sweden, except for a number of recoveries of birds ringed at Falsterbo (Roos 1983). It is based on recoveries made until the end of 1982, including many of those already published by Rendahl (1959).

Most Great Tits ringed as nestlings and recovered the following autumn or winter moved moderate distances (Figs. 1 and 3), those from the southern half of Sweden in a predominantly south-westerly direction. Most Great Tits recovered in presumed winter quarters in Denmark originate from South Sweden, but two birds come from further north. Records made more than 1 year after ringing (Figs. 2 and 3) show a much more scattered picture, probably reflecting both northward movements after the first winter and a SW-directed autumn migration also in later years (on average 9% of the Great Tits caught at Falsterbo in autumn are more than 1 year old; Lindskog & Roos 1979, G. Roos in litt.). The recoveries of Great Tits ringed in winter quarters (Figs. 4–6) show a picture similar to Fig. 1 and 3, but with direction of movements reversed. Thus, most of the recoveries of birds ringed in southernmost Sweden (and in Denmark) come from South Sweden; six recoveries indicate that a proportion of Great Tits from northernmost Scandinavia may winter in South Central Sweden. Fig. 7 present recoveries of Great Tits ringed in September and October, i.e. during the normal migration period. Again Skåne and Denmark seem to be the main wintering area of birds ringed in South Sweden. An unknown proportion of the Great Tits ringed at the coastal observatories (Ottenby, Torhamn and Utklippan) is likely to originate from areas east of the Baltic (Lindholm 1978 and Tab. 1), and this may also be true of birds at Svenska Högarna, as Great Tits ringed in the Soviet Baltic Republics have been found in SW Finland.

The recoveries of Blue Tits ringed as nestlings (Fig. 8) differ from those of Great Tits in that (1) a somewhat larger proportion have moved long distances and (2) there is a clear component of movements towards the north-west, both features also apparent from Fig. 9, which shows recoveries of Blue Tits ringed during the autumn migration period. The few recoveries (seven in all) of Blue Tits ringed in winter give little additional information.

Litteratur

- Alerstam, T. 1982. *Fågelflyttning*. Lund.
van Balen, J.H. & Speek, B.J. 1976. Een Invasie van Mezen (*Paridae*) in de Herfst van 1971. *Limosa* 49: 188–200.
Berndt, R. & Henss, M. 1963. Die Blaumeise, *Parus c. caeruleus* L., als Invasionsvogel. *Vogelwarte* 22: 93–100.

- Edelstam, C. & Österlöv, S. 1969. Ringmärkningsmetoden – den ornitologiska forskningens lyckokast. *Fauna & Flora* 64: 207–219.
Efremov, V. 1975. (Age and sex composition of the Great Tit (*Parus major* L.) during autumn migration over the Curland Spit.) *Comm. Baltic Commission Study Bird Migr.* 9: 83–90 (på ryska med engelsk sammanfattning).
Hansen, K. 1978. Track og spredning hos danske Musvitter *Parus major*. *Dansk orn. Foren. Tidskr.* 72: 97–104.
Kastepöld, T. & Kabal, R. 1977. Estonia matsalu 1976. Ringing Report No. 7. *Loodusvaatlusi* 1976 (2): 4–134.
Lindholm, C.-G. 1978. Talgoxens sträck över Östersjön höstarna 1975 och 1976. *Anser, Suppl.* 3: 145–153.
Lindskog, H. & Roos, G. 1979. Höststräckets förlopp hos blåmes *Parus caeruleus* och talgoxe *Parus major* vid Falsterbo 1973–1978. *Anser* 18: 171–188.
Lipsbergs, J. & Rute, J. 1975. (Autumn migration of tits of the family *Paridae* and the Long-tailed Tit on the south-west coast of Latvia in 1967–1971.) *Comm. Baltic Commission Study Bird Migr.* 9: 105–122 (på ryska med engelsk sammanfattning).
Mohr, R. 1962. Ergebnisse der Beringung deutscher Blaumeisen (*Parus caeruleus*). *Vogelwarte* 21: 210–219.
Perrins, C.M. 1979. *British Tits*. London.
Pettersson, J. 1981. Rugging och geografiskt ursprung hos talgoxar *Parus major* vid Ottenby. *Vår Fågelv.* 40: 461–466.
Plattner, J. & Sutter, E. 1946–47. Ergebnisse der Meisen- und Kleiber-beringung in der Schweiz (1929–1941). *Orn. Beob.* 43: 156–188, 44: 1–35.
Rendahl, H. 1959. Die Wanderungen der schwedischen Meisen. *Bonn. zool. Beitr.* 10: 351–386.
Roos, G. 1983. Flyttning, övervintring och livslängd hos fåglar märkta vid Falsterbo 1947–1980. *Anser, Suppl.* 13.
Thielemans, L. & Eyckerman, R. 1975. Migration and mortality in the Blue Tit (*Parus c. caeruleus* L.). *Biol. Jb. Dodonaea* 43: 252–265.
Ulfstrand, S. & Högstedt, G. 1976. Hur många fåglar häckar i Sverige. *Anser* 15: 1–32.
Ulfstrand, S., Roos, G., Alerstam, T. & Österdahl, L. 1974. Visible migration at Falsterbo, Sweden. *Vår Fågelv., Suppl.* 8.
Österlöv, S. 1964–1980. (Årsrapporter från Ringmärkningscentralen vid Naturhistoriska riksmuseet, publicerade i *Vår Fågelvärld* och *Vår Fågelvärld, Suppl.* samt som fristående publikationer/Annual Reports from the Bird Ringing Office, the Swedish Museum of Natural History, published in *Vår Fågelv., Vår Fågelv., Suppl.*, and as monographs.)

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Appendix 1. Märk- och återfyndsdata för talgoxar märkta under sträcktid om hösten, figur 7. Numreringen svarar mot numreringen i denna.

Ringning and recovery data for Great Tits ringed during the autumn migration period.

a. Märkta vid Hammarön, Nidingen, Svenska Högarna, m.fl. platser

1.	2 476 091	1K+	♂	74.10.02	!/?	(75.01.07)	Kvånum (58.18 N, 13.11 E)
2.	2 759 720	1K	♂	81.10.06	+K	81.10.29	Tynnered (57.39 N, 11.53 E)
3.	2 443 570	1K+	♀	73.09.16	x	73.10.15	Kungshamn (58.22 N, 11.15 E)
4.	2 438 329	1K+	♀	72.10.08	v	75.02.06	Oslo (59.56 N, 10.40 E)
5.	2 807 075	1K	♂	81.10.11	x	(82.01.02)	Dröbak (59.40 N, 10.40 E)
6.	2 625 784	1K+	♀	77.10.12	x	78.04.17	Lågsjär (59.50 N, 19.56 E)
7.	2 827 028	1K	♀	81.09.28	v	81.10.02	Signilskär (60.12 N, 19.20 E)
8.	2 587 502	1K+	♂	76.10.05	+K	77.01.17	Fagersta (59.59 N, 15.48 E)
9.	2 827 032	1K+	♀	81.09.28	v	82.03.27	Gilbjerg Hoved (56.08 N, 12.17 E)
10.	2 827 061	1K+	♀	81.09.29	v	82.10.03	Hartso-Enskär (58.41 N, 17.29 E)
11.	3 053 772	1K+	♀	61.10.22	()	63.01.15	Matrand (60.01 N, 12.08 E)
12.	3 117 425	2K+?		64.10.21	v	67.04.21	Moldford (67.00 N, 14.35 E)
13.	2 236 715	1K+	♀	66.10.06	x	66.10.26	Kalmar (56.40 N, 16.20 E)
14.	2 550 948	2K+	♀	76.10.21	v	77.03.31	Jämeda (59.01 N, 25.42 E)

b. Märkta vid Ottenby

1.	2 579 898	1K+	♀	76.10.21	v	76.11.04	Christiansö (55.19 N, 15.12 E)
2.	2 595 269	1K	♀	76.10.23	v	76.10.26	ibidem
3.	2 595 406	1K	♂	76.10.24	v	76.11.09	ibidem
4.	2 520 844	1K	♂	75.10.21	x	75.11.06	Leba (54.45 N, 17.32 E)
5.	2 424 561	1K	♂	72.10.11	x	72.12.31	St. Karlsö (56.12 N, 16.31 E)
6.	2 738 087	1K	♀	80.10.11	x	80.12.17	Köpingsvik (56.53 N, 16.43 E)
7.	2 094 691	2K+	♂	62.10.01	x	62.12.22	Skelebjerg (55.32 N, 11.26 E)
8.	2 158 679	1K	♂	64.10.14	xA	65.04.15	S. Rörum (55.57 N, 13.42 E)
9.	ZOB 5 874			49.10.17	x	49.11.29	Tystofte (55.14 N, 11.19 E)
10.	2 158 100	1K		64.09.25	+K	(65.10.28)	Verkeback (57.44 N, 16.31 E)
11.	2 579 959	1K	♂	76.10.21	x	77.11.25	litti (60.59 N, 26.21 E)

c. Märkta vid Falsterbo och Ljunghusen

1.	2 795 790	1K	♀	81.10.13	v	81.10.26	Bukowa-Kopan (54.28 N, 16.25 E)
2.	2 720 509	1K	♀	81.09.26	+K	(81.11.18)	Karise (55.18 N, 12.13 E)
3.	2 790 837	1K	♀	81.10.13	+K	(82.02.02)	8 km S Aabenraa (55.00 N, 09.25 E)
4.	2 795 149	1K	♀	81.10.11	x	(82.02.18)	Saerslev (55.32 N, 10.12 E)
5.	2 720 766	1K	♀	81.10.06	x	(82.02.27)	Jystrup (55.31 N, 11.53 E)
6.	2 795 165	2K+	♀	81.10.11	x	81.10.24	Holbaek (55.43 N, 11.43 E)
7.	2 720 171	1K	♀	81.09.23	x	(82.02.03)	Kongelunden (55.35 N, 12.35 E)
8.	2 795 541	1K	♀	81.10.13	v	82.01.16	Olofström (56.14 N, 14.38 E)
9.	2 444 735	1K	♂	73.10.11	x	(77.11.21)	Skede (57.30 N, 15.08 E)
10.	2 540 873	1K	♀	75.10.05	v	75.10.08	Kloster/Hiddensee (54.36 N, 13.07 E)
11.	3 140 707	1K	♀	65.10.02	v	65.11.14	Ivenack (53.43 N, 12.59 E)
12.	3 140 721	1K	♂	65.10.09	+K	(65.12.03)	Värnamo (57.11 N, 14.02 E)
13.	2 543 203	1K	♀	75.10.12	x	(77.03.08)	Figeholm (57.22 N, 16.33 E)
14.	2 639 858	1K	♀	77.10.30	x	79.04.13	Kulhuse (55.56 N, 11.55 E)

d. Märkta vid Torhamn, Utklippan och Karlskrona

1.	2 617 318	1K	♀	77.10.03	v	77.10.14	Christiansö (55.19 N, 15.12 E)
2.	2 703 734	1K	♂	80.10.10	v	80.10.13	ibidem
3.	2 526 501	1K		75.09.30	v	75.11.11	Zoutleeuw (50.50 N, 05.06 E)
4.	2 645 865	1K	♂	78.10.07	x	79.02.04	Gylle (55.24 N, 13.12 E)
5.	3 054 341	1K+		61.10.11	v	61.11.24-1	Klippan (56.07 N, 13.09 E)
6.	2 703 935	1K	♂	80.10.20	x	81.03.29	Markaryd (56.28 N, 13.36 E)
7.	3 118 915	1K+		63.10.06	x	63.11.10	Lund (55.42 N, 13.11 E)
8.	3 112 890	2K+?		63.09.24	v	63.10.20	Hvidovre (55.39 N, 12.28 E)
9.	2 645 752	1K	♀	78.10.05	x	78.10.23	Hartso-Enskär (58.41 N, 17.29 E)

Appendix 2. Märk- och återfyndsdata för blåmesar märkta under sträcktid om hösten, figur 9. Numreringen svarar mot numreringen i denna.

Ringning and recovery data for Blue Tits ringed during the autumn migration period.

a. Märkta på olika platser i Götaland och Svealand

1.	2 721 714	1K	80.09.26	v	80.10.16	Falsterbo (55.23 N, 12.50 E)
2.	2 721 771	1K	80.09.27	x	(81.05.11)	Soon (59.32 N, 10.42 E)
3.	2 697 390	1K	79.10.07	x	80.04.21	Mellan Björkelangen och Aurskog (59.55 N, 11.30 E)
4.	2 464 079	1K	73.09.30	x	74.04.14	Österdalen (61.06 N, 11.20 E)
5.	2 697 723	1K	79.10.21	(x)	80.06.11	Torsby (68.08 N, 13.03 E)
6.	2 464 134	1K	73.10.01	+K	75.12.13	Sunnemo (59.53 N, 13.43 E)
7.	2 572 940	1K	77.10.14	+K	80.06/07	Millesvik 58.58 N, 13.06 E)
8.	2 755 262	1K	80.10.01	v	80.10.26	Falsterbo
9.	2 819 047	1K	81.10.17	x	81.11.21	Ängelholm (56.15 N, 12.52 E)
10.	1 858 299	1K	75.10.07	x	75.11.11	30 km N Rörös (62.51 N, 11.17 E)
11.	1 664 926	2K+	73.10.02	x	73.10.24	Staberg (60.34 N, 15.47 E)
12.	2 347 510	1K	70.09.27	v	71.04.03	Ljungsbro (58.31 N, 15.30 E)
13.	2 104 631	1K	62.09.29	x	62.11.09	Råbelöv (56.05 N, 14.11 E)
14.	2 207 305	1K	65.09.25	x	67.01.00	Ballerup (55.44 N, 12.22 E)
15.	2 437 341	1K	74.09.01	xA	76.08.00	Rostock (54.06 N, 12.09 E)
16.	2 747 885	1K	81.10.13	v	81.10.19	Utklippan (55.57 N, 15.42 E)

b. Märkta vid Ottenby

1.	2 541 357	1K	75.10.02	v	75.10.03	Utklippan
2.	2 784 487	1K	81.09.24	v	81.10.01	ibidem
3.	2 738 014	1K	80.10.09	v	80.10.14	Christiansö (55.19 N, 15.12 E)
4.	2 424 639	2K+	72.10.11	v	72.10.14	Bukowo (54.21 N, 16.17 E)
5.	2 784 726	1K	81.10.01	v	81.10.25	Rybachi (55.08 N, 20.42 E)

c. Märkta vid Torhamn och Utklippan

1.	2 527 159	1K	75.10.05	x	76.04.04	Grenå (56.25 N, 10.53 E)
2.	2 415 310	1K+	72.09.16	!/?	(73.01.13)	Veksö (55.45 N, 12.14 E)
3.	2 487 791	1K	74.09.11	v	74.09.26	Beddinge (55.22 N, 13.26 E)
4.	2 101 081	1K+	62.10.06	!/?	65.01.03	Sandvig (55.18 N, 14.46 E)
5.	2 527 689	1K	75.10.24	x	76.03.06	Löttorp (57.09 N, 16.59 E)
6.	2 410 190	1K	73.09.01	x	(74.06.13)	Houens Ode (55.31 N, 09.35 E)

Population fluctuations of some North European bird species in relation to winter temperatures

Variationer i storlek hos några nordeuropeiska fågelpopulationer i förhållande till vintertemperaturen

Hans Källander and Johnny Karlsson

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För många nordeuropeiska fåglar är det välkänt, att extremt hårda vintrar orsakar nedgångar i de häckande populationerna. I denna uppsats analyserar vi närmare sambandet mellan vintertemperaturen och antalet häckande par den efterföljande säsongen. Det är ett generellt samband mellan vinterns hårdhet och populationsstorleken efterföljande säsong för arter som talgoxe, blåmes, nötväcka och koltrast. Det är således inte bara extremt hårda vintrar som påverkar populationerna, utan sambandet finns kvar även under "milda vintrar".

Temperaturen i sig är naturligtvis inte den reglerande faktorn – den är bara ett sätt att mäta tillgång på föda, den mängd energi fåglarna gör av med, osv. Att födan är en viktig faktor framgår när tillgången på bokollon, en omtyckt föda för mesar under vintern, har korrelerats med populationsstorleken. För flera arter framstår sambandet mellan födotillgång och överlevnad tydligt.

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Introduction

Most studies dealing with the effect of winter temperatures on the fluctuations of bird populations have concentrated on the impact of extremely hard winters (e.g., Ticehurst and Witherby 1940, Berndt 1941, Jespersen 1941, Ticehurst and Hartley 1948, Berndt and Frantzen 1964, Dobinson and Richards 1964, and literature cited in these papers). Berndt (1941) found a marked decline in numbers of several species of tits *Parus* spp. after the two severe winters of 1928/29 and 1939/40, and Berndt and Frantzen (1964) found a similar decline after the likewise very severe winter of 1962/63. After the same winter, Simms (1965) recorded only half the usual number of Blackbirds *Turdus merula* in a London suburb while a number of other species in Britain, especially some species associated with water and wetlands, were also affected (Dobinson and Richards 1964). The Grey Heron *Ardea cinerea* population of England and

Wales has shown marked declines after cold winters (Reynolds 1979).

Although it seems well established that unusually cold winters negatively influence the winter survival and the size of the subsequently breeding populations of a number of bird species, few studies have analysed the relation between winter temperatures and population fluctuations in more detail. Kluijver (1951) correlated the difference in the number of breeding Great Tits *Parus major* in the Netherlands from one year to the next (which he termed the 'disparity') with winter temperatures and obtained a moderately good correlation during a 31-year period, whereas Lack (1966) found no such correlation in the Great Tit population of Marley Wood near Oxford. Balen (1976), also in the Netherlands, found a positive correlation between the number of breeding Great Tits and preceding winter temperatures for the years 1968–1974 but not for the

period 1960–1966, Gibb (1960), studying Coal Tits *Parus ater* in a pine plantation in eastern England, found that their winter survival correlated strongly with mean air temperatures during January to March. Based on data from 16 years at Lemsjöhölm in south-eastern Finland, von Haartman (1971) presented a close correlation between the number of Great Tits breeding in his nest-boxes and the mean temperature of the preceding December to February. Likewise Karlsson and Källander (1977) found a significant correlation between the severity of the winter and the size of the Blackbird population subsequently breeding in a suburban study area at Lund, South Sweden.

Slagsvold (1975) reanalysed the population changes of tits in Marley Wood near Oxford and in Forest of Dean in Gloucestershire as well as those at Lemsjöhölm using linear correlations. He varied both the length of the period during which temperatures were allowed to act and the starting date for the periods. In this way he obtained results that showed how the correlation coefficient varied, e.g. with different starting dates. He was thus able to identify those temperature periods which correlated most strongly with population changes and which were therefore most likely to be biologically significant.

In the present paper we analyse the influence of winter temperatures on the size of the subsequent breeding populations of Great Tits and Blue Tits *Parus caeruleus* at two localities in Skåne, South Sweden, and on that of Blue Tits and Nuthatches *Sitta europaea* near Braunschweig in Germany. In addition we supplement our earlier data on the suburban Blackbird population at Lund and analyse the British Grey Heron data.

Population data, method of analysis

Data on the size of the breeding population of Great and Blue Tits were obtained from (1) a nest-box study carried out by Sten Svensson in an oak-wood at Rynke near Ljungbyhed (55°06'N, 13°15'E) during 1958–1978, (2) a similar study at Linnebjerg near Lund (55°44'N, 13°18'E) between 1969 and 1978 (for details, cf. Källander 1976), and (3) (for the Blue Tit) data from Germany for 1954–1978 published by Berndt and Winkel (1979). Nuthatch data covering the period 1955–1978 were taken from the latter source. The Blackbird population of a suburban area at Lund (55°42'N, 13°11'E) (Karlsson and Källander 1977) was subjected to census for another four years and the new data included here, while information on the Grey Heron population of England and Wales was taken from Reynolds (1979).

The size of the breeding population of each species and each locality was plotted for each year against an index of the coldness of the preceding winter, and linear regression is calculated. Winter index is defined as the

summed monthly deviations from the long-term means for the months December to March. This index rather than mean temperatures (which yield exactly the same correlations) was used to make graphs from different areas directly comparable. The data for the Grey Heron were, however, analysed against the mean temperatures for the months December to February.

Winter temperature data were obtained from official weather statistics. For the analysis of the tit populations at Rynke and Linnebjerg, and of the Blackbird population at Lund, meteorological data from Lund were used, while data from Braunschweig were used for the Blue Tit and Nuthatch populations in Germany. For the Grey Heron, temperature data from central England were taken from Lamb (1977). The long-term mean at Lund is 1.9°C for December, -0.7 for January, -0.8 for February, and 1.3 for March. Corresponding figures for Braunschweig are 0.9, -0.1, 0.3 and 3.7°C.

Mean temperatures are, of course, but one aspect of the severity of a winter and not necessarily the most important one to the birds. It has, however, the advantage of being simple to quantify and a number of other variables, e.g. the number of days with temperatures below zero and with snow cover, correlate with mean temperatures.

Results

Figs 1–4 present the regressions of population size on preceding winter temperatures except for the British Grey Heron. All populations vary positively with winter temperatures. The correlation coefficients for the Blackbird, the Nuthatch, the Blue Tit in Germany, and the Great Tit at Rynke reach different levels of statistical significance while those for the Blue Tit at Rynke and Linnebjerg, and for the Great Tit at Linnebjerg only approach statistical significance at the 5% level (Tab. 1).

In a slowly or fairly slowly reproducing species, one year's production, however good, cannot immediately compensate a population decline; more years are needed to bring the population back to previous numbers. In such species, therefore, one cannot expect a good agreement between winter temperatures and the size of the subsequent breeding population. This situation obviously applies to the Grey Heron; here, a further complication is that the birds may take more than one year to reach maturity (Bauer and Glutz 1966). In agreement with this, the correlation coefficient for all years included in Reynold's (1979) paper was 0.47 ($n = 50$, $p < 0.001$), but when the correlation was restricted to years when the population declined (and the effect of a slow reproduction eliminated), a very strong correlation with winter temperatures emerged ($r = 0.86$, $n = 17$, $p < 0.001$).

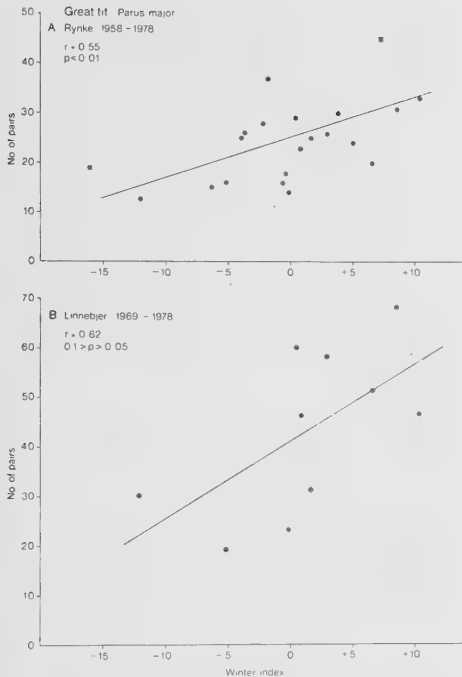


Fig. 1. Regressions of the size of breeding populations of the Great Tit *Parus major* on the temperatures of the preceding winter (December to March).
 Populationsstorlek hos talgöxe i förhållande till temperaturen under den föregående vintern (december-mars).

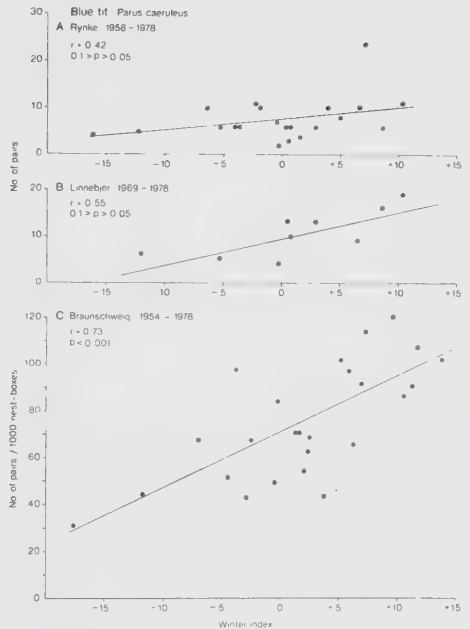


Fig. 2. Regressions of the size of breeding populations of the Blue Tit *Parus caeruleus* on the temperatures of the preceding winter (December to March).
 Populationsstorlek hos blåmes i förhållande till temperaturen under den föregående vintern (december-mars).

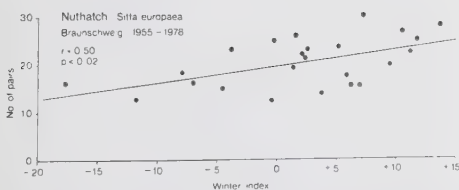


Fig. 3. Regression of the size of a breeding population of the Nuthatch *Sitta europaea* on the temperatures of the preceding winter (December to March).
 Populationsstorlek hos nötväcka i förhållande till temperaturen under den föregående vintern (december-mars).

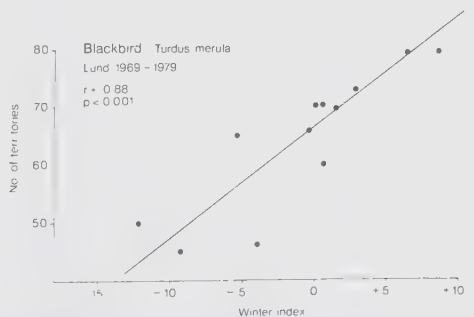


Fig. 4. Regression of the size of a breeding population of the Blackbird *Turdus merula* on the temperatures of the preceding winter (December to March).
 Populationsstorlek hos koltrast i förhållande till temperaturen under den föregående vintern (december-mars).

Tab. 1. Correlation coefficients (r) and significance levels (p) for the relation between the size of breeding populations of the Great Tit *Parus major*, the Blue Tit *P. caeruleus*, the Nuthatch *Sitta europaea* and the Blackbird *Turdus merula* and the temperatures during different periods of the preceding winter, at localities in South Sweden and North Germany. Korrelationskoefficienter (r) och signifikansnivåer (p) för sambandet mellan populationsstorlek och temperaturen under skilda delar av den föregående vintern för talgoxe, blåmes, nötväcka och koltrast på några lokaler i södra Sverige och norra Tyskland.

		December–March		February		March	
		r	p	r	p	r	p
Great Tit	Rynke	0.55	<0.01	0.45	<0.05	0.59	<0.01
Great Tit	Linnebjerg	0.62	<0.10	0.70	<0.05	0.59	<0.01
Blue Tit	Rynke	0.42	<0.10	0.42	<0.10	0.39	<0.10
Blue Tit	Linnebjerg	0.55	<0.10	0.62	<0.10	0.74	<0.02
Blue Tit	Braunschweig	0.73	<0.001	0.47	<0.05	0.58	<0.01
Nuthatch	Braunschweig	0.50	<0.02	0.34	<0.10	0.29	>0.10
Blackbird	Lund	0.88	<0.001	0.41	>0.10	0.70	<0.02

Discussion

The results presented above support Haartman's (1971) finding for the Great Tit at Lemsjöholm that not only do extremely cold winters negatively affect the size of the subsequent breeding population, but populations of some species tend to fluctuate in parallel with winter temperatures within the whole temperature range. Apart from the Great Tit, this applies to the Blue Tit, the Nuthatch, the Blackbird, the Grey Heron and possibly other species as well (cf. Svensson 1981). If this relation is causal, one may ask in what way, or ways, do winter temperatures affect the birds.

Firstly, lower ambient temperatures increase a bird's energy requirements, which is probably more important to small birds with their less favourable energy balance. Secondly, lower temperatures may reduce the availability of the birds' prey. This is obviously the case for the suburban Blackbirds at Lund: in mild winters they are often able to feed on earthworms, but when ambient temperatures decrease below some 2°C these become unavailable and the Blackbirds may be forced to feed on food of lower quality such as various fruits (Karlsson pers. obs.). Low temperatures are also likely to influence the activity of insects and spiders making them less available to birds like tits and Nuthatches (Betts 1955), but part of their invertebrate food consists of inactive stages (eggs, pupae). Low temperatures also tend to correlate with the presence of snow; the effect of a snow cover is to reduce the availability of food on the ground. This not only affects the Blackbird, but also the tits, especially the Great Tit, which forages to a considerable extent on the ground (Perrins 1979). For the Grey Heron, one would assume the presence or absence of ice to be a decisive factor.

The suburban Blackbirds, however, rely to a varying degree on food put out by people; because more food is almost certainly provided during severe winters, the ef-

fect would be to reduce their negative influence on the Blackbird population.

Correlations with other temperature periods

Slagsvold (1975) obtained the highest correlation coefficients for the relation between temperature and the relative change in size of the Great Tit populations in Marley Wood and the Forest of Dean during the period 7 March to 15 April, while at Lemsjöholm the best fit was during the period 2 February to 13 March. To see if similar results would be obtained, we calculated regressions using only the mean temperatures in February and March respectively. As seen from Tab. 1, the correlation coefficients improved compared to those for the whole winter period for the Great and Blue Tits at Linnebjerg, was about the same for these two species at Rynke, decreased somewhat for the Blue Tit in Germany and decreased considerably for the Nuthatch and the Blackbird. Why then were stronger correlations obtained in some cases when the analysis was restricted to late winter and early spring?

At least two, strongly contrasting explanations are possible. One is that the end of the winter is the most critical period for the birds because non-renewing food supplies have been continually reduced in the course of the winter and reach their lowest level at this time. This explanation is supported by the direct measurements of food levels that Gibb (1960) carried out as part of his study of Coal Tits in pinewood. Here, the food levels decreased considerably during the winter. It is also supported by the observation that a substantial proportion of the available food is actually taken by the birds themselves during the winter (Askenmo et al. 1977). On the other hand, Jansson et al. (in press) in their study of winter survival in Willow Tits *Parus montanus* and Crested Tits *P. cristatus* found no bottlenecks during the period December to start of breeding.

The second explanation was put forward by Krebs

(1971) who found a positive correlation between the size of the breeding population of Great Tits in Marley Wood at Oxford and February temperatures when he kept the adult: juvenile ratio constant in a partial regression. His interpretation was that temperatures influenced the pattern of territory establishment: low temperatures, he suggested, would lead to a gradual occupation of territories, whereas high temperatures would result in a more simultaneous occupation. The latter process would allow more territories on a given area (in accordance with the findings of Assem (1967) on Sticklebacks *Gasterosteus aculeatus* and also the models later presented by Maynard Smith (1974) and Knapton and Krebs (1974)).

At present it seems impossible to choose between these two hypotheses, but some support for the former comes from winter feeding experiments. Balen (1975) and Källander (manuscript) reported higher breeding density of Great Tits in experimental plots where food had been provided during winter. One would not expect this result if temperatures in early spring determined breeding density through territorial behaviour, at least not if they were the only determinants. We therefore believe, at least provisionally, that winter temperatures act on the birds predominantly through their effects on food availability, and that the effects are strongest at the end of the winter (although the results for the Nuthatch and the Blackbird (Tab. 1) do not support the latter suggestion).

Other causes of fluctuations

Although the size of the subsequent breeding populations of the bird species studied in this paper correlates positively with temperatures during the preceding winter, a large part of the variation remains unexplained. The best correlation with winter temperatures was shown in the Blackbird; in this species almost 80% of the variation is explained by temperature. The weakest correlation was shown in the Nuthatch, where only a quarter of the variation is explained by temperature. The tits fall somewhere between these extremes.

It has been known for a long time that the size of the breeding populations of the Great Tit correlates strongly with the size of the beech mast crop of the preceding autumn (Perrins 1965). This relation may be indirect, however, because populations of Great Tits have been claimed to fluctuate in parallel with beech mast also in areas with no beech (Perrins 1979). This question no doubt requires further study, but considering the extensive use of beech mast in winter by the tits (Ulstrand 1962, Perrins 1965), it seems likely that a casual link exists between this food source and fluctuations in tit numbers.

Beech mast data are available from Denmark for the years considered in this paper. As the beech mast crop is known to vary synchronously over large areas (Perrins 1965, 1966), these data may be used to look for a possible influence of beech mast abundance on the fluctua-

Tab. 2. Correlation between fluctuations in the Great Tit *Parus major*, the Blue Tit *P. caeruleus*, and the Nuthatch *Sitta europaea* breeding populations and beech mast abundance during the preceding winter (beech mast data from Denmark; Statsskovvaesenet, Statsskovenes Planteavlstation).

Korrelation mellan fluktuationer hos talgoxe, blåmes och nötväcka och tillgången på bokollon. (Uppgifter om bokollonförekomst har erhållits från Statsskovenes Planteavlstation, Danmark.)

		Correlation coefficient r_s	Significance level p
Great Tit	Rynke	0.41	<0.05
Great Tit	Linnebjerg	0.42	ns
Blue Tit	Rynke	0.57	<0.01
Blue Tit	Linnebjerg	0.02	ns
Blue Tit	Braunschweig	0.65	<0.01
Nuthatch	Braunschweig	0.42	<0.05

tions of the tit and Nuthatch populations studied here. There are limitations, however, that restrict the usefulness of beech mast data as discussed by Perrins (1966). Perhaps the most important one is that the crop size is presented on an arbitrary scale (in Denmark ranging from 0 = no mast to 4 = very rich crop), whose intervals may not be equal. Therefore, it is necessary to use a non-parametric correlation method (Spearman rank). The results of such an analysis show that, apart from varying in response to winter temperatures, some populations also tended to fluctuate in relation to beech mast abundance (Tab. 2). Thus, both the Great and Blue Tits at Rynke and the Blue Tits in Germany showed significant correlations with beech mast, as did the Nuthatches. At Linnebjerg, however, neither Great Tit or Blue Tit fluctuations were significantly correlated with beech mast. As expected, there was no positive correlation between Blackbird numbers and beech mast abundance.

On the whole variations in the winter temperature in North Europe explain a large part (approx 80%) of the population fluctuations in the Blackbird. Even for the Great Tit, the Blue Tit and the Nuthatch there is a positive correlation, in some cases statistically significant, between the winter temperature and the size of the breeding populations.

Finally, we wish to emphasize that there must be no long-term trends in the populations analysed in the way that we have done. If there are such trends it is advisable to use percentage change from year to year, thus accepting the disadvantages connected with that method.

Acknowledgements – We wish to express our deep gratitude to Sten Svensson for putting his long series of data at our disposal and to H. Barner, Statsskovvaesenet, Humlebaek, Denmark for help with data on the beech mast production. U. Högström, Inst. of Meteorology, Univ. of Uppsala, kindly provided temperature data for Braunschweig.

	Great tit <i>Parus major</i>		Blue tit <i>Parus caeruleus</i>		Blackbird <i>Turdus merula</i>	Beech mast crop in the preceding autumn
	Rynke	Linnebjerg	Rynke	Linnebjerg	Lund	
1954	—	—	—	—	—	1
1955	—	—	—	—	—	4
1956	—	—	—	—	—	0
1957	—	—	—	—	—	4
1958	15	—	10	—	—	0
1959	30	—	10	—	—	1
1960	18	—	7	—	—	0
1961	45	—	21	—	—	3
1962	28	—	11	—	—	0
1963	19	—	4	—	—	0
1964	25	—	6	—	—	0
1965	37	—	10	—	—	3
1966	26	—	6	—	—	0
1967	24	—	8	—	—	0
1968	16	—	3	—	70	1
1969	16	19	6	5	65	0
1970	13	30	5	6	50	1
1971	23	46	6	10	60	1
1972	26	58	6	13	73	1
1973	31	68	6	16	79	0
1974	20	51	10	9	79	1
1975	33	46	11	19	—	3
1976	14	23	2	4	66	0
1977	29	60	6	13	70	4
1978	25	31	5	5	69	0
1979	—	—	—	—	45	0
1980	—	—	—	—	46	0

References

- Askenmo, C., Brömssen, A. von, Ekman, J. and Jansson, C. 1977. Impact of some wintering birds on spider abundance in spruce. — *Oikos* 28: 90–94.
- Assem, J. van den. 1967. Territory in the three-spined stickleback (*Gasterosteus aculeatus*). — *Behaviour*, Suppl. 16: 1–164.
- Balen, J. H. van. 1975. Factors affecting the size of the breeding population. — *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk.*, Tweede Reeks 66: 80.
- 1976. Factors affecting the size of the breeding population. — *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk.*, Tweede Reeks 67: 3–5.
- Bauer, K. M. and Glutz, U. N. 1966. *Handbuch der Vögel Mitteleuropas*. Bd 1. — Akad. Verlagsgesellschaft, Frankfurt a. M.
- Berndt, R. 1941. Über die Einwirkung der strengen Winter 1928/29 und 1939/40 und den Einfluss der Winterfütterung auf den Brutbestand der Meisen. — *Die gefiederte Welt* 70: 59–61, 63–65, 80–81, 91–92, 101–103, 117–118.
- and Frantzen, M. 1964. Vom Einfluss des strengen Winters 1962/63 auf den Brutbestand der Höhlenbrüter bei Braunschweig. — *Orn. Mitt.* 16: 126–130.
- and Winkel, W. 1979. Zur Populationsentwicklung von Blaumeise (*Parus caeruleus*), Kleiber (*Sitta europaea*), Gartenrotschwanz (*Phoenicurus phoenicurus*) und Wendehals (*Jynx torquilla*) in mitteleuropäischen Untersuchungsgebieten vom 1927 bis 1978. — *Vogelwelt* 100: 55–69.
- Betts, M. M. 1955. The food of titmice in oak woodland. — *J. Anim. Ecol.* 24: 282–323.
- Dobinson, H. M. and Richards, A. J. 1964. The effect of the severe winter of 1962/63 on birds of Britain. — *Brit. Birds* 57: 373–434.
- Gibb, J. A. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. — *Ibis* 102: 163–208.
- Haartman, L. von. 1971. Population dynamics. — In: Farner, D. and King, J. (eds.), *Avian Biology*. Vol. 1. Acad. Press, New York; pp. 391–459.
- Jansson, C., Ekman, J. and Brömssen, A. von. Winter mortality and food supply in tits, *Parus* spp. — *Oikos* (in press).
- Jespersen, P. 1941. The effect of the winter of 1939–40 upon the stock of breeding birds in Denmark. — *Dansk Ornithol. For. Tidskr.* 35: 66–78. (In Danish with summary in English.)
- Källander, H. 1976. Data on the breeding biology of the Blue Tit *Parus caeruleus* and the Marsh Tit *P. palustris* in southwest Scania. — *Vår Fågelvärld* 35: 1–7. (In Swedish with summary in English.)
- The effects of provision of food in winter on a population of the Great Tit *Parus major* and the Blue Tit *P. caeruleus*. — (Manuscript.)
- Karlsson, J. and Källander, H. 1977. Fluctuations and density of suburban populations of the Blackbird *Turdus merula*. — *Ornis Scand.* 8: 139–144.
- Kluijver, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. — *Ardea* 39: 1–135.

- Knapton, R. W. and Krebs, J. R. 1974. Settlement patterns, territory size, and breeding density in the song sparrow (*Melospiza melodia*). – Can. J. Zool. 52: 1413–1420.
- Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. – Ecology 52: 2–22.
- Lack, D. 1966. Population studies of birds. – Clarendon Press, Oxford.
- Lamb, H. H. 1977. Climate. Present, past and future. Volume 2, Climatic history and the future. – Methuen, London.
- Maynard Smith, J. 1974. Models in Ecology. – Cambridge Univ. Press, Cambridge.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major*. – J. Anim. Ecol. 34: 601–647.
- 1966. The effect of beech crops on Great Tit populations and movements. – Brit. Birds 59: 419–432.
- 1979. British Tits. – Collins, London.
- Reynolds, C. M. 1979. The heronries census: 1972–1977 population changes and a review. – Bird Study 26: 7–12.
- Simms, E. 1965. Effects of the cold weather of 1962/63 on the Blackbird population of Dollis Hill, London. – Brit. Birds 58: 33–43.
- Slagsvold, T. 1975. Critical period for regulation of Great Tit (*Parus major* L.) and Blue Tit (*Parus caeruleus* L.) populations. – Norw. J. Zool. 23: 51–72.
- Svensson, S. 1981. Populationsfluktuationer hos mesar *Parus*, nötväcka *Sitta europaea* och trädskrypare *Certhia familiaris* i södra Sverige (Population fluctuations in tits *Parus*, Nuthatch *Sitta europaea*, and Treecreeper *Certhia familiaris* in South Sweden). – Proc. Second Nordic Congr. Ornithol. 1979: 9–18.
- Ticehurst, N. F. and Hartley, P. H. T. 1948. Report on the effect of the severe winter of 1946–7 on bird-life. – Brit. Birds 41: 322–334.
- and Witherby, H. F. 1940. Report on the effect of the severe winter of 1939–40 on bird-life in the British Isles. – Brit. Birds 34: 118–132, 142–155.
- Ulfstrand, S. 1962. On the nonbreeding ecology and migratory movements of the Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) in southern Sweden. – Vår Fågelv., Suppl. 3: 1–145.

The effects of provision of food in winter on a population of the Great Tit *Parus major* and the Blue Tit *P. caeruleus*

Hans Källander

Källander, H. 1981. The effects of provision of food in winter on a population of the Great Tit *Parus major* and the Blue Tit *P. caeruleus*. – *Ornis Scand.* 12: 244–248.

To study the influence of the food supply in winter on populations of Great and Blue Tits, food was provided in study plots during two winters. After the first winter, Great Tits increased in the experimental plots whereas they decreased in control areas. After the second winter when beech mast was present, the number of Great Tits increased in all areas; the increase was no larger in the experimental plots than in the controls. A higher proportion of first year birds survived (or stayed) in the experimental woods than in a control. The Blue Tit population seemed unaffected by the provision experiment.

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Introduction

Lack (1966) argued that populations of tits *Parus* spp. are regulated by food in winter, the time of year when it is most likely to be in short supply. Irrespective of whether food regulates populations of tits, i.e. acts in a density dependent way, or not, a number of studies have shown that populations of the Great Tit *Parus major* and the Blue Tit *P. caeruleus* tend to fluctuate in parallel with the beech mast crop (Perrins 1979), an important food source during winter (Ulfstrand 1962). These fluctuations may be taken to indicate that winter food levels affect winter survival and, at least partly, determine the size of the subsequent breeding populations (which incidentally, are the ones normally correlated with beech mast abundance). The relation between the population fluctuations of the tits and the seed production of the beech is, however, complicated. Both Lack (1966) and Perrins (1979) state that parallel fluctuations in tit numbers occur also in areas outside the range of the beech and conclude that any correlation between beech mast abundance and tit numbers must be indirect. They presented no data in support of synchronous fluctuations in beech and non-beech areas, however, and the question no doubt calls for further study.

To study the effects of winter food on the subsequent breeding populations of Great and Blue Tits, in the winters of 1969–70 and 70–71, food (mainly sunflower seeds) was provided in the two study areas in SW Skåne, a third area being left as a control.

Study areas and method

The study was carried out in three deciduous woods near Lund in SW Skåne: Linnebjerg (experimental; oak-dominated, approx. 24 ha), Frueråften (experimental; separated from Linnebjerg only by 500 m of agricultural land, dominated by mature beech and young oak-sycamore plantations; approx. 19 ha), and Dalby Norreskog (control; 10 km further south, varied: one portion containing mature oak, one part beech, but most of the wood either young planted oak-sycamore or mixed semi-natural ash, alder, and oak; approx. 17 ha). All areas contained 6–7 nest-boxes ha⁻¹.

As further controls I used population data on the Great Tit from Rynke near Ljungbyhed (about 40 km north of Linnebjerg; Sten Svensson pers. comm.) and from North Germany (Berndt and Winkel 1974) and for the Blue Tit, data from Rynke (Sten Svensson pers.

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comm.), Sörön in South Central Sweden (Johannesson 1976), and North Germany (Berndt and Winkel 1979).

In the winter of 1969–70, experimental provision of food started in Linnebjerg in the beginning of December and in Frueraften ten days later. Sunflower seeds were provided at fifteen feeding tables in Linnebjerg and at seven in Frueraften; in addition open tins containing fat with sunflower seeds were attached to some 40 trees in each of the two woods. In late February and early March these feeding stations were supplemented with a total of about 70 large hoppers with sunflower seeds. In the winter of 1970–71, the provision of food was restricted to Linnebjerg. It started already by mid-October, but the tits probably did not take the seeds until late November or early December. Forty-seven hoppers of a better design replaced the old ones from 6 December. Provision of sunflower seeds continued through March. In that winter, however, the hoppers were rather irregularly utilized and possibly mostly by finches (Greenfinches *Carduelis chloris* and Bramblings *Fringilla montifringilla* in particular).

The beech mast crop, winter temperatures, and snow cover

For a number of years from the late 1960s until autumn 1974, the size of the beech mast crop seems to have varied between different places in South Sweden in the same year. Although no really large crop occurred during that period, one area or another experienced a weak or moderate crop during several of the years. Unfortunately, official Swedish data on the production of beech seeds are not available after 1961–62, but the Danish crop was classified as more or less nil in 1968–69 and 1972–73, and poor in 1969–70, 1970–71, and 1971–72 (Statsskovvaesenet, Statsskovenes Planteavlstation). In Frueraften, some beech seeds were present in the winter of 1969–70, and the crop in the following winter was fairly rich both there and in Dalby Norreskog (and in many other places as well).

The winter of 1969–70 was very severe with temperatures far below average (the temperature deficit for the period December to March was 12.9°C at Lund) and with a snow cover from the end of December that lasted through March. Snow storms and low temperatures were again experienced in late March and the first week of April. The beech mast present in Frueraften could be utilized by the tits only to the extent that Pheasants *Phasianus colchicus* had dug holes through the snow; this was observed in mid-December. Otherwise, any beech seeds still present in winter were largely unavailable. In contrast, the winter of 1970–71 was average with almost no snow. The fairly rich beech mast crop was therefore available to the tits; in Dalby Söderskog, a wood adjacent to Dalby Norreskog, tits were still seen taking beech seeds in mid-March and they probably also did so elsewhere.

Results

In the three control areas, the Great Tit populations decreased after the severe winter of 1969–70, whereas they increased by 58 and 18%, respectively, in Linnebjerg and Frueraften, where food had been provided (Tab. 1). After the following winter (1970–71), they increased by between 35 and 94% in all areas regardless of whether they had been supplied with extra food or not. In fact, the increase was relatively largest in Dalby Norreskog where no extra food had been provided (Tab. 1).

For the Blue Tit (Tab. 2), where numbers were very low, there was an increase from five to six pairs in Linnebjerg between 1969 and 1970, but in Frueraften numbers decreased from five to two pairs. The population decreased in all control areas. After the winter of 1970–71, the population rose in all areas except in Dalby Norreskog where it remained at four pairs.

In the woods with extra winter food, adult survival of Great Tits was high in Linnebjerg, especially between 1969 and 1970, while it was remarkably low in Frueraften both between 1969 and 1970 and between 1970 and 1971. In the untreated Dalby Norreskog, adult survival was intermediate between that in Linnebjerg and Frueraften in 1969–70 and higher than that in Linnebjerg in 1970–71 (Tab. 3). Yearling survival

Tab. 1. The number of pairs of the Great Tit *Parus major* breeding in two areas where winter food was experimentally provided (Linnebjerg and Frueraften, see text), and in three control areas during 1969–71. The per cent change from the previous breeding season is given in parenthesis. Data for Rynke from Sten Svensson (pers. comm.) and for North Germany from Berndt and Winkel (1974).

	1969	1970	1971
Linnebjerg	19	30 (+57.9)	46 (+53.3)
Frueraften	17	20 (+17.6)	27 (+35.0)
Dalby Norreskog . .	19	17 (–10.5)	33 (+94.1)
Rynke	16	13 (–18.8)	23 (+76.9)
N. Germany	35	31 (–11.4)	47 (+51.6)

Tab. 2. The number of pairs of the Blue Tit *Parus caeruleus* breeding in two areas where winter food was experimentally provided (Linnebjerg and Frueraften, see text), and in four control areas during 1969–71. For North Germany, a population index is given. Data for Rynke from Sten Svensson (pers. comm.), for Sörön from Johannesson (1976), and for North Germany from Berndt and Winkel (1979).

	1969	1970	1971
Linnebjerg	5	6	10
Frueraften	5	2	6
Dalby Norreskog	5	4	4
Rynke	6	5	6
Sörön	10	5	14
N. Germany	51.45	44.09	70.77

Tab. 3. Proportion of adult and yearling Great Tits *Parus major* surviving locally in the three study woods from 1969 to 1970 and from 1970 to 1971, respectively. Adult refers to birds caught while breeding, yearling to birds ringed as nestlings. The number of birds controlled breeding in the following year is given in brackets for each category. In 1971 only females were controlled and yearling survival was calculated assuming equal sex ratio in the nest. Food was provided in Linnebjerg and Frueraften in winter 1969–70 and in Linnebjerg in 1970–71.

	1969–70		1970–71	
	Adults	Yearlings	Adults	Yearlings
Linnebjerg	0.59 (20)		0.37 (11)	
Frueraften	0.13 (4) ¹¹	0.141 (42)	0.19 (3)	0.216 (43)
Dalby Norreskog	0.35 (13)	0.066 (39)	0.47 (9)	0.108 (9)

¹¹ In 1970, five nests were deserted before the identity of the parents could be determined. Therefore the true survival rate in Frueraften may have been higher.

rates, or emigration rates, differed between the populations provided with food (Linnebjerg and Frueraften) on the one hand and the unfed Dalby Norreskog population on the other; more yearlings remained where food had been provided (Tab. 3).

The proportion of immigrants (unringed birds from outside the study areas) was somewhat higher in Frueraften than in Linnebjerg and Dalby Norreskog; although perhaps underestimated, a low adult survival rate in Frueraften was probably the main reason for the much smaller population increase there between 1969 and 1970 compared to Linnebjerg (18% increase against 58%). Also between 1970 and 1971, when the Great Tit populations rose in all areas, the increase was proportionally smallest in Frueraften; obviously, somehow Frueraften was a less good habitat for tits.

Discussion

Why did the provision of food in winter 1969–70 result in an increase in the number of subsequently breeding Great Tits compared to control populations, whereas the provision of food (in Linnebjerg) in winter 1970–71 had no similar effect? As mentioned above, the winter of 1969–70 was very severe with much snow that remained for a long period and with little or no beech mast available to the tits, while the winter of 1970–71 was slightly milder than average with almost no snow. During the latter winter, the birds were thus able to utilize the fairly rich beech mast crop that was present. Balen (1976) in his study area near Arnhem in the Netherlands, found that the effect of provision of food in winter decreased with an increasing beech mast crop. With a poor crop, the effect of supplemental food was to double the per cent survival of both adults and yearlings. By contrast, in a good beech mast year, there was no effect of supplemental food. Adults responded more strongly to the provision of food in a poor beech mast year and reached nearly as high a survival rate as in a good mast year, while yearlings did not attain the high survival rate of a good mast year. Thus, the lack of a

difference in the rate of population increase between (Linnebjerg (experimental) and the other areas after the winter of 1970–71 agrees with Balen's results. However, in the experimental populations, survival was high between 1969 and 1970 only in Linnebjerg (in fact even higher than between 1970 and 1971), not in Frueraften, although food was provided in both woods. The reason for this is unknown.

Food provision increased the proportion of yearlings which remained and bred (Tab. 3). Whether this reflects an increased survival due to the provision of extra food or a higher emigration rate of birds from Dalby Norreskog is not known (yearling birds are likely to travel between the adjacent Linnebjerg and Frueraften woods, so yearlings from Frueraften no doubt also had access to supplemental food provided in Linnebjerg in the winter of 1970–71). Dalby Norreskog is a little less isolated from other wooded areas than are Linnebjerg and Frueraften.

In contrast to the Great Tits, the Blue Tits did not increase after the provision of food (Tab. 2). This is contrary to the results of Krebs (1971). In the winter of 1968–69, P. R. Jones and J. R. Krebs supplied sunflower seeds to Great and Blue Tits in Bean Wood near Oxford. A comparison of population trends in Bean Wood and nearby Marley Wood (control) revealed no effect on the Great Tits, which showed a similar slight increase in both woods. The Blue Tits, however, increased in Bean Wood whereas they decreased in Marley Wood. Krebs concluded that the availability of winter food probably has no influence on the breeding density of the Great Tit, whereas it has on that of the Blue Tit.

The different results obtained in the two studies are surprising. I think that if the provision of sunflower seeds in winter positively influences populations of tits, one would predict a stronger influence on the Great Tit than on the Blue Tit, because seeds constitute a larger proportion of the winter diet of the former species (Betts 1955, Ulfstrand 1962). This was illustrated in the winter of 1979–80 when sunflower seeds were provided at a hopper and spread out on the snow in an alder

wood facing lake Krankesjön, SW Skåne. Whereas large numbers of Great Tits were attracted to the seeds only one Blue Tit was caught despite the fact that large Blue Tit parties were simultaneously feeding on insects and spiders in the *Phragmites* reeds only some 30 m away (pers. observ.). This difference in diet was also pointed out by Krebs (1971). However, fat, a food often eaten by Blue Tits in winter, was also provided in my study; nevertheless my results for the Blue Tit are negative or at least inconclusive.

The effect of supplemental winter food on populations of Great and Blue Tits has been treated in more general terms by Berndt (1941), Berndt and Frantzen (1964), and Haartman (1973). Haartman (1973) recorded larger breeding populations of the Great Tit in three years after supplemental winter feeding than expected from a regression of population size on winter temperatures, but could not tell whether this resulted from a better survival of local birds or from immigration. Berndt (1941), studying the effects of the severe winters of 1928–29 and 1939–40 on tits, the Nuthatch *Sitta europaea*, and the Treecreeper *Certhia familiaris*, suggested that the provision of food in winter may have influenced some populations positively. His conclusion was not based on experiments however, but on the fact that populations near Leipzig, where food was put out for the birds, showed a much smaller decrease than populations further from human habitations. In one fed area, the numbers even rose despite a decrease in all other areas, but here also more nest-boxes were put up; the effect of this cannot be evaluated from Berndt's paper. Suggestive data on the positive influence of supplemental food on Great Tit numbers also come from Berndt & Frantzen's (1964) report on the effects of the severe winter of 1962–63 on hole-nesting passerines near Braunschweig. Food was richly supplied in four out of 17 study areas. The population of Great Tits decreased by between 3 and 72% in all 13 unfed areas (except in one, where more nest-boxes were put up, and the number of Great Tits rose from nine to ten pairs). In those areas where food was provided, the population decreased by 15% in one, remained stable in two, and increased by 44% in one. In contrast, the Blue Tit decreased, often by as much as 70%, in all areas except the one with more nest-boxes; here the number of breeding pairs rose from 14 to 15. These data seem to contradict Krebs' (1971) conclusion and support my finding that Blue Tits were unaffected by the provision of food during winter whereas Great Tits were not.

A number of studies have been carried out to study the effect of experimental provision of food in winter on populations of other species of tits, e.g., Deadman (1973) on the Coal Tit *Parus ater*, Samson and Lewis (1979) on the Black-capped Chickadee *P. atricapillus* and the Tufted Tit *P. bicolor*, Jansson et al. (1981) and Hogstad (pers. comm.) on the Willow Tit *P. montanus*. Deadman (1973) found no clear effect of winter feeding on the breeding population of Coal Tits in Scotland al-

though the winter population was as much as 6–7 times denser in the fed plot than in the unfed control plot (Deadman pers. comm.). Samson and Lewis (1979) found only a small increase in the number of breeding Black-capped Chickadees despite an increased number of birds in the winter flocks; no differences were found in the Tufted Tit. In Hogstad's experiment on Willow Tits at Baerum near Oslo, the population in March was significantly larger in the areas where food was provided during winter than in a control area, and he concludes that provision of food in winter had a positive effect on survival in the Willow Tit. Also the numbers breeding in the experimental plot were somewhat higher, but the difference was too small to be statistically significant. A clear positive effect was however obtained in the carefully conducted experiment of Jansson et al. (1981), which involved large number of birds. Both immigration rate and survival rate were influenced; the latter almost doubled in the experimental plots. Although the disappearance rate was higher in the experimental plots in the period immediately after the provision of food ended in early April, their breeding populations were considerably denser than that of the control area. Thus, it seems that the food supply in winter determines, at least to a considerable extent, the subsequent breeding density of Willow Tits (Jansson et al. 1981) and Great Tits (Balen 1975, present study), thus supporting Lack's (1966) suggestion that food levels in winter are limiting. The same may be true also for other species of tits, even if the winter feeding experiments carried out so far have given negative or uncertain results (with the possible exception of an apparent effect on Blue Tits at Oxford; Krebs 1971). This is however, not to say that territorial behaviour in spring does not act in a density dependent way or that it has no regulatory effect, only that any such effect is weak, a conclusion also reached by Krebs and Perrins (1978) for the Great Tit.

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References

- Balen, J. H. van 1975. Factors affecting the size of the breeding population. – Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Reeks 66: 80.
- 1976. Factors affecting the size of the breeding population. – Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Reeks 67: 106–109.
- Berndt, R. 1941. Über die Einwirkung der strengen Winter 1928/29 und 1939/40 und den Einfluss der Winterfütterung auf den Brutbestand der Meisen. – Die gefiederte Welt 70: 59–61, 63–65, 80–81, 91–92, 101–103, 117–118.

- and Frantzen, M. 1964. Vom Einfluss des strengen Winters 1962/63 auf den Brutbestand der Höhlenbrüter bei Braunschweig. – Orn. Mitt. 16: 126–130.
- and Winkel, W. 1974. Ökoschema, Rivalität und Dismigration als öko-ethologische Dispersionsfaktoren. – J. Orn. 115: 398–417.
- and Winkel, W. 1979. Zur Populationsentwicklung von Blaumeise (*Parus caeruleus*), Kleiber (*Sitta europaea*), Gartenrotschwanz (*Phoenicurus phoenicurus*) und Wendehals (*Jynx torquilla*) in mitteleuropäischen Untersuchungsgebieten von 1927 bis 1978. – Vogelwelt 100: 55–69.
- Betts, M. M. 1955. The food of titmice in oak woodland. – J. Anim. Ecol. 24: 202–223.
- Deadman, A. J. 1973. A population study of the Coal Tit (*Parus ater*) and the Crested Tit (*Parus cristatus*) in a Scottish Pine plantation. – Ph.D. thesis, Aberdeen University.
- Haartman, L. von 1973. Talgmespopulationen på Lemsjöholm. – Lintumies 8: 7–9.
- Jansson, C., Ekman, J. and Brömssen, A. von 1981. Winter mortality and food supply in tits (*Parus* spp.). – Oikos 37 (in press).
- Johannesson, H. 1976. Häckfågelinventeringen i Sörön, Kvismaren 1965–1974. – Fauna Flora 71: 15–28.
- Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. – Ecology 52: 2–22.
- and Perrins, C. 1978. Behaviour and population regulation in the Great Tit (*Parus major*). – In: Ebling, F. J. and Stoddart, D. M. (eds.). Population control by social behaviour. Institute of Biology, London.
- Lack, D. 1966. Population studies of birds. – Clarendon Press, Oxford.
- Perrins, C. M. 1979. British Tits. – Collins, London.
- Samson, F. B. and Lewis, S. J. 1979. Experiments on population regulation in two North American parids. – Wilson Bull. 91: 222–233.
- Ullstrand, S. 1962. On the nonbreeding ecology and migratory movements of the Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) in southern Sweden. – Vår Fågelvärld, suppl. 3.

A note on divorce frequency, breeding dispersal, and the role of age in the choice of mate in the Great Tit *Parus major*

It has been known for a long time that older females of the Great tit *Parus major* lay a larger clutch and raise more young to fledging than do first year females (Kluijver 1951, Perrins 1965). Recently, Harvey et al. (1979) showed that the age of the male likewise has an influence on the breeding performance. Although their results were not unequivocal with regard to the number of young fledged and the number of young subsequently found breeding, mean clutch size was significantly higher in matings between older than in matings between first year individuals, being intermediate in matings between older and first year birds. Perrins (1965) also found a higher post-fledging survival of young raised by older than by yearling parents. In view of these results one would predict that older individuals should mate preferentially with other older individuals.

In the Kittiwake *Rissa tridactyla* mates are more prone to divorce after a breeding failure (Coulson 1972), and Winkel (1975) found that, whereas only 12 % of female Great Tits changed mate between successful breeding attempts in the same season, three out of four unsuccessful females bred with a new mate. However, divorces should only occur when the partner has shown a poor capacity in raising young and the chances are good to do better with a new mate.

Here I test, on a limited material from a nest-box study of Great Tits in a rather isolated 24 ha large oak wood (Linnebjerg) near Lund, South Sweden, (i) whether birds that remate after a divorce increase their fitness, and (ii) if there is a bias towards matings between older individuals. In addition some data on distances of breeding dispersal (Harvey et al. 1979a) are given. Unfortunately, males were not ringed every year; most data therefore refer to the seasons 1969/70 and 1972/73. The number of older and first year birds found in the breeding population was used to calculate expected mating frequencies assuming random mating among them (or a section of them).

RESULTS

Divorces

In a total of 32 cases where both partners survived to the following breeding season they bred together again in 20 (62 %) and divorced in 12 (38 %). Corresponding figures in Kluijver's study (1951) were 77.5 and 22.5 % ($n = 71$), while Harvey et al. (1979a) estimated that 30 % of the pairs in the Wytham Great Tit population divorced each year. In Saitou's (1979) study in Japan only 15 % of surviving pairs divorced ($n = 53$), and the proportion was lower in birds that stayed in the study area during the winter than in those that left and returned again in spring.

In 1973, of 28 females breeding also in 1972, 9 bred with the same male, 9 had changed partner despite their former mate still being alive, and 10 were paired with a new male after the disappearance of their former mate. The number of males with new females after (probably) having become widowers were 12. Thus about a third of the birds divorced between 1972 and 1973. Did the divorcing pairs have a low breeding success in 1972? This was not the case: pairs that broke up after the 1972 breeding season did so despite producing slightly more ($\bar{x} = 9.33$), not fewer, young than the rest of the pairs ($\bar{x} = 8.78$); and 29.8 % of their fledglings survived more than 3 months vs. 23.5 % of the young of the other pairs. Neither difference is, however, statistically significant.

Did divorcing birds improve their production of fledglings after remating? Since the mean number of fledglings produced varies between years, data must be normalised, i.e. expressed as a deviation from each year's mean. Faithful birds on average increased the number of fledglings produced by 0.39 (S.D. 3.39, $n = 13$). In birds that had remated after a divorce, the corresponding figure was 0.57 (S.D. 1.96, $n = 11$) for females and - 0.66 (S.D. 2.82, $n = 10$) for males. In the males, 2 did better after remating and 8 worse, whereas in females 8 did better and 3 worse ($p = 0.04$, Fisher Exact).

The post-fledging survival in 1973, measured as the proportion of young recaptured more than 3 months after fledging, was 20.3 % (30 of 148) for young from pairs formed after a divorce, 30.6 % (22 of 72) for young from faithful pairs, and 27.4 % (88 of 321) for young from the rest of the population. Thus, there was a slight tendency ($p < 0.1$, χ^2) that young of pairs formed after a divorce had lower post-fledging survival than young of other pairs.

Distance between subsequent breedings

Usually birds that changed mate between seasons, despite their former mate being alive, bred in the vicinity of the territory of the previous year. This applies to both males and females, but females tended to move a little longer (median 85 m, range 0 - 241 m, $n = 11$) than males (50, range 0 - 61 m, $n = 9$), the difference being statistically significant ($p < 0.01$, median test, Fisher Exact). Also in widowed birds females moved longer than males: 117 m (range 0 - 384 m, $n = 27$) vs. 54 m (range 0 - 115, $n = 19$), $p < 0.02$, median test, χ^2 . Pairs that remained together moved 43 m (range 0 - 109 m, $n = 15$). Thus, in this study, males moved similar distances from one year to the next (c. 50 m) regardless of whether they remained paired to the same female or remated after a divorce or the disappearance of their partner. Females, in contrast, moved longer distances if they had divorced or become widowed.

Do Great Tits prefer experienced mates?

Assuming that the birds that subsequently bred in the wood were those available at the time of pair formation, did pairs form at random? The answer is no. In both years from which data exist, there were too many matings between older individuals and too few between older individuals and first year birds ($p < 0.05$, χ^2). The same bias is found in the data of Saitou (1979). If, however, birds that remained faithful are excluded as done by Greenwood et al. (1979a), the observed mating frequencies among the rest of the birds closely agree with expected values (> 0.6).

Of the 9 females that divorced between 1972 and 1973, 7 paired with a male younger than themselves (5 of which first year birds), 1 with a male of the same age, and 1 with a male of unknown age. Of the males, 5 paired with females younger than themselves (first year birds), 1 with a female of the same age, and 1 with an older female. For 2 males data are lacking.

Due to the small sample size, a more detailed analysis of the mating birds' status, i.e. whether residents or immigrants, as carried out by Greenwood et al. (1979a) and Saitou (1979), gave inconclusive results.

DISCUSSION

The limited material of this study does not point to any proximate factor causing mates to divorce and remate with a new partner.

Neither fledging success nor post-fledging survival was poorer for pairs that subsequently broke up, rather there was some indication that the opposite was true. However, it appeared that females more often increased their production of young after a divorce and mating with a new partner, while the reverse was true of males. One hypothesis, therefore, is that females tend to leave males that have not taken their proper share in feeding young; there seems to be a rather large variation between males in this respect (pers. obs.). If so, however, it was reflected neither in the production of fledglings nor in the post-fledging survival of the latter.

Both divorced and widowed females had longer median dispersal distances (85 and 117 m, respectively) from one season to the next compared to faithful females (50 m), and to males regardless of category (50 m). This differs from the results of Harvey et al. (1979a) who observed no difference in dispersal distance between widowed and faithful females, whereas divorced females tended to move longer.

As in the study of Greenwood et al. (1979a), there was no age bias in the mating frequencies observed when pairs that remained together were excluded, i.e. there was no indication that older birds sought out other older (divorced or widowed) birds in the wood; the existence of this kind of selectivity, predicted from the higher productivity of such matings (Harvey et al. 1979), was not supported.

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REFERENCES

- Coulson, J.C. 1972. The significance of the pair-bond in the Kittiwake. *Proc. XV Int. Orn. Congr.*: 424-433.
- Greenwood, P.J., Harvey, P.H. & Perrins, C.M. 1979. The role of dispersal in the Great Tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *J. Anim. Ecol.* 48: 123-142.
- Greenwood, P.J., Harvey, P.H. & Perrins, C.M. 1979a. Mate selection in the Great Tit *Parus major* in relation to age, status and natal dispersal. *Ornis Fennica* 56: 75-86.

- Harvey, P.H., Greenwood, P.J., Perrins, C.M. & Martin, A.R. 1979. Breeding success of Great Tits Parus major in relation to age of male and female parent. Ibis 121: 216-219.
- Harvey, P.H., Greenwood, P.J. & Perrins, C.M. 1979a. Breeding area fidelity of Great Tits (Parus major). J. Anim. Ecol. 48: 305-313.
- Kluijver, H.N. 1951. The population ecology of the Great Tit, Parus m. major L. Ardea 39: 1-135.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the Great Tit (Parus major). J. Anim. Ecol. 34: 601-647.
- Saitou, T. 1979. Ecological study of social organization in the Great Tit, Parus major L. IV. Pair formation and establishment of territory in the members of basic flocks. Misc. Rep. Yamashina Inst. Orn. 11: 172-188.
- Winkel, W. 1975. Vergleichend-bruthiologische Untersuchungen an fünf Meisen-Arten (Parus spp.) in einem niedersächsischen Forstungsgebiet mit Japanischer Lärche Larix lepolepis. Vogelwelt 96: 41-63, 104-114.

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